Variation des traits le long des gradients environnementaux : rôle de l'intégration phénotypique et de la variabilité au sein des clades

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Introduction générale

I. De quoi parlons-nous ?

I.1. Définition d'un trait

Un trait correspond à toutes caractéristiques morphologiques, physiologiques ou phénologiques mesurables au niveau de l'individu, de la cellule à l'organisme, sans référence à l'environnement ou à tout autre niveau d'organisation (Violle et al. 2007). La valeur particulière prise par un trait dans un environnement à un temps donné est appelée « attribut » (Lavorel et al. 1997). L'attribut d'un trait est généralement évalué à l'échelle de la population (moyenne des attributs d'un groupe d'individus de la même espèce) pour un environnement à un temps donné. Si la variabilité du trait est faible à l'intérieur d'une espèce et forte entre les espèces (par exemple, mode de reproduction uniquement sexué chez presque tous les individus d'une espèce), il est possible d'attribuer une valeur unique de ce trait à l'espèce.

A l'intérieur d'une espèce, un trait peut présenter différents attributs le long d'un gradient environnemental ou au cours du temps. L'ensemble des attributs pris par les traits d'un individu dans un environnement à un temps donné constitue son phénotype. En cela, le phénotype constitue l'ajustement fonctionnel d'un individu à son environnement (Crawford 2008). Les traits peuvent être contraints par les variations de l'environnement, aussi bien dans leur valeur moyenne que dans leur variance. Mais les traits peuvent aussi être contraints par (i) l'intégration phénotypique (interdépendance des traits) au sein d'un organisme (Schlichting 1989b) et par (ii) les contraintes sur la variabilité phénotypique exprimés dans un clade entier (Cavender-Bares et al. 2009). Nous reviendrons précisément sur ces notions dans la suite de l'introduction.

I.2. Définition de l'environnement

L'environnement est défini comme l'ensemble des éléments qui entourent un individu (par exemple, une plante). On distingue l'environnement abiotique qui correspond aux éléments non-vivants de l'environnement (par exemple, climat et conditions édaphiques). L'environnement abiotique a une action directe sur les traits des plantes. On sait par exemple que les plantes de haute altitude ont un cycle de reproduction très court, limité aux périodes sans neige (Ladinig & Wagner 2005). Les espèces des milieux secs développent des feuilles petites et succulentes pour limiter l'évaporation de l'eau et vont en moyenne présenter une plus faible surface spécifique foliaire (*Specific Leaf Area*) (Larcher 2003). On peut connaître l'environnement abiotique occupé par une plante au moyen de mesures *in situ* des conditions abiotiques qui l'entourent, mais aussi en caractérisant sa tolérance en termes d'habitat (par exemple, tolérance à l'ombrage, à la salinité ou à la sécheresse). L'environnement biotique correspond aux éléments vivants de l'environnement qui entrent en interaction avec la plante (par exemple, compétiteurs, mutualistes ou phytophages). Les interactions biotiques influencent également les traits des plantes. Un exemple connu est l'ajustement des caractères de la fleur aux pollinisateurs (Navarro et al. 2007).

II. L'étude de la variation des traits avec l'environnement

II.1. La moyenne des attributs de traits

Comprendre comment les individus ajustent leurs traits aux contraintes de l'environnement mobilise depuis longtemps les chercheurs en écophysiologie, écologie de la conservation et écologie évolutive. Les recherches se sont d'abord essentiellement focalisées sur l'étude de la moyenne des attributs de traits à l'échelle des espèces (Thuiller et al. 2004a ; Wright et al. 2005a, b), des clades (Moles et al. 2005) ou des communautés (Ackerly & Cornwell 2007 ; Pellissier et al. 2010). La valeur moyenne des attributs d'un trait peut refléter différents

aspects de la biologie des individus, comme la survie, la croissance, la reproduction ou la dispersion, tous paramètres dépendants de la disponibilité en ressources et des contraintes climatiques dans un environnement à un temps donné (Grime 2001 ; Cronin & Lodge 2003 ; Willis & Hulme 2004).

L'étude de la moyenne des attributs de traits a notamment permis de mettre en évidence des stratégies écologiques des plantes (Grime 1977 ; Westoby 1998), d'établir des types fonctionnels de végétation (Raunkiær 1934; Ellenberg 1988 ; Smith et al. 1997) et des classifications fonctionnelles des plantes (Lavorel et al. 1997) ainsi que de caractériser les réponses écophysiologiques des individus aux contraintes environnementales (par exemple, croissance, reproduction, survie) (Larcher 2003). Plus récemment, elle a permis d'estimer l'évolution d'un trait (ou la coévolution de plusieurs traits) à l'intérieur d'une lignée (Moles et al. 2005 ; Westoby et al. 2002 ; Wright et al. 2007). Cependant, l'étude de la moyenne des attributs de traits est largement insuffisante pour décrire l'ensemble des processus intervenant dans l'ajustement des traits à l'environnement. Des études récentes montrent que des mesures de variabilité des traits sont indispensables à une meilleure compréhension des processus d'ajustement des traits à l'environnement (Albert et al. 2010a,b).

II.2. Variabilité intraspécifique des attributs de traits

Les recherches se sont ensuite élargies à l'étude de la variabilité intraspécifique des attributs de traits (Reich et al. 2003 ; Richards et al. 2005 ; Thuiller et al. 2010). La variabilité intraspécifique est définie par Albert et al. (2010a) comme « la gamme de valeurs d'un trait qui peut être réalisée, mais aussi la variabilité de ce qui est fonctionnellement expérimenté par les individus d'une espèce donnée dans différentes conditions environnementales ». La variabilité intraspécifique résulte de la diversité génétique et de la plasticité phénotypique de différents génotypes, les deux étant potentiellement complémentaires et non exclusifs (Byars

et al. 2007). Elle peut se mesurer (i) à l'échelle d'une population comme la différence entre les traits des individus de la population ou (ii) à l'échelle de plusieurs populations comme la différence entre les moyennes des traits au sein de populations occupant des conditions environnementales contrastées (Albert et al. 2010a).

La variabilité intraspécifique des attributs de traits a surtout été étudiée pour déterminer les compromis entre fonctions (i.e. *trade-offs*, Reich et al. 2003) et pour quantifier les réponses fonctionnelles des espèces aux gradients environnementaux (Richards et al. 2005 ; Thuiller et al. 2010). Une grande variabilité intraspécifique pourrait permettre aux individus d'une espèce de survivre, de croître et de se reproduire dans de nouvelles conditions environnementales (Byars et al. 2007). Elle pourrait ainsi définir la gamme écologique et géographique d'une espèce (Valladeres et al. 2002) et jouer un rôle dans la réponse des populations et des espèces aux changements environnementaux (Albert et al. 2010a). Cependant, nous verrons dans les chapitres suivants que la variabilité intraspécifique seule ne reflète pas la nature complexe des réponses phénotypiques aux variations environnementales. Les interactions complexes entre traits (intégration phénotypique, voir § III.1.1. de l'Introduction générale) et entre conditions environnementales occupées par les espèces (intégration environnementale, voir § III.1.2. de l'Introduction générale) devraient également être considérées pour mieux comprendre et prédire la capacité de réponse des espèces aux variations de l'environnement. De même, certains auteurs concluent sur l'importance de compléter les mesures de variabilité intraspécifique par des mesures de variabilité interspécifique (Albert et al. 2010b).

II.3. Variabilité interspécifique des attributs de traits

De manière similaire à la variabilité intraspécifique (Albert et al. 2010a), on peut définir la variabilité interspécifique comme la gamme de valeurs d'un trait qui peut être réalisée, mais

aussi la variabilité de ce qui est fonctionnellement expérimenté par les espèces d'un groupe donné (par exemple, communauté ou clade) dans différentes conditions environnementales. Elle peut se mesurer comme la différence entre les moyennes du trait des espèces du groupe.

La variabilité interspécifique a été essentiellement étudiée pour quantifier la diversité fonctionnelle des communautés (de Bello et al. 2009) ou pour estimer les divergences fonctionnelles à différents nœuds de la phylogénie (Moles et al. 2005). Elle a également permis de mesurer les changements de diversité fonctionnelle des communautés le long des gradients environnementaux (Ricklefs & Travis 1980 ; Stevens et al. 2003 ; Ackerly & Cornwell 2007 ; Swenson & Enquist 2007). Enfin, certaines études ont porté sur la structure phylogénétique des communautés, c'est-à-dire sur le rôle des relations phylogénétiques entre les espèces dans leur assemblage au sein des communautés (Prinzing et al. 2008 ; Cavender-Bares et al. 2009). Cependant, nous ignorons à peu près complètement les raisons pour lesquelles, au sein d'une région, certains clades ont des traits beaucoup plus variables que d'autres clades. Par exemple, nous ne savons pas si la variabilité interspécifique réalisée au sein des clades d'une région donnée diffère selon l'environnement qu'ils occupent. Nous ne savons pas non plus si de telles différences reflèteraient des processus d'assemblage des espèces inhérents à leur appartenance à certains clades.

II.4. Corrélation entre les traits et l'environnement

Dans l'ensemble, une forte corrélation entre les traits et l'environnement implique que la gamme de variabilité de traits exprimée par une espèce ou un groupe d'espèces (par exemple, communauté ou clade) à un moment donné est fortement investie dans un ajustement étroit des traits à l'environnement. Une corrélation entre les traits et l'environnement ne peut être mise en évidence que s'il existe une certaine variabilité de traits et d'environnements au sein de l'espèce ou du groupe d'espèces. Une telle corrélation peut se mesurer (i) sur les individus

d'une même population, (ii) sur plusieurs populations occupant des environnements différents ou (iii) sur plusieurs espèces.

La corrélation entre les traits et l'environnement a été beaucoup étudiée afin de comprendre l'influence de l'environnement sur le phénotype. Elle a par exemple permis de déterminer, parmi un ensemble de facteurs environnementaux, celui qui va le plus influencer la valeur d'un trait chez un individu (par exemple, Murray et al. 2003). Elle a également permis de mettre en évidence des filtres environnementaux qui conditionnent localement l'assemblage des espèces (Cavender-Bares et al. 2009). Enfin, elle a permis de mieux comprendre comment un facteur environnemental (abiotique ou biotique) a pu influencer l'évolution d'un trait au sein d'une lignée (Moles et al. 2005 ; Futuyama & Agrawal 2009). Cependant, des corrélations entre les traits et l'environnement ne sont pas systématiquement mises en évidence au sein des espèces. Ceci pourrait notamment résulter du fait que ces corrélations sont conditionnées par la gamme de variabilité des traits et des environnements occupés par les espèces. Cela pourrait également avoir comme origine le fait que la plupart des études sur les corrélations entre les traits et l'environnement ne prennent pas en compte les interactions complexes qui existent entre les traits au sein d'un individu (intégration phénotypique, voir § III.1.1. de l'Introduction générale) et entre les conditions environnementales occupées par les espèces (intégration environnementale, voir § III.1.2. de l'Introduction générale). Des mesures de variabilité intraspécifique et d'intégration du phénotype et de l'environnement devraient donc compléter les mesures de corrélation entre les traits et l'environnement, afin mieux comprendre les processus d'ajustement des traits à l'environnement. Finalement, la plupart des études sur les corrélations entre les traits et l'environnement ne prennent pas en compte le fait que la variabilité des traits peut différer entre les clades.

III. Aspects peu étudiés de la variation des traits avec l'environnement

III.1. L'intégration phénotypique et environnementale au sein des espèces

III.1.1. Définition de l'intégration phénotypique

L'intégration phénotypique correspond au niveau d'interdépendance des traits au sein d'un individu. Elle est plus généralement définie comme la force et le nombre des corrélations entre les traits d'un individu (Schlichting 1989b, Pigliucci & Marlow 2001). Elle est plus rarement définie comme le niveau de variabilité multivariée des traits au sein d'un individu (Rapson & Maze 1994). L'intégration s'estime théoriquement à l'échelle d'une ou plusieurs populations (Schlichting 1989a ; Pigliucci 2003) et peut se généraliser à l'espèce (Rapson & Maze 1994). Il a été démontré qu'une forte intégration phénotypique entre un ensemble de traits peut refléter une forte intégration des gènes qui codent pour ces traits (Waitt & Levin 1998). La coévolution de traits d'importance écologique (par exemple, hauteur de la plante et dispersion des graines) peut constituer le résultat d'une adaptation par des pressions de sélection favorisant la combinaison de certains traits. Dans ce cas, le jeu de traits inter-corrélés forme une *dimension de stratégie écologique* (Westoby et al. 2002 ; Reich et al. 2003 ; Wright et al. 2007). Il a également été montré qu'une forte intégration phénotypique peut refléter une faible plasticité phénotypique (Gianoli & Palacio-Lopez 2009), c'est-à-dire une faible capacité des individus à modifier leur expression phénotypique en réponse aux variations de l'environnement au cours de leur vie (West-Eberhard 2003). Enfin, une forte intégration phénotypique peut résulter d'une haute intégration plastique (Schlichting 1989a), c'est-à-dire d'un fort degré de similitude entre les réponses plastiques de plusieurs traits (Schlichting & Levin 1986). L'intégration phénotypique pourrait donc dériver à la fois de processus évolutifs sur le long terme et sur le court terme (Reich et al. 2003). En résumé, un renforcement des corrélations entre traits dans un environnement donné pourrait refléter une augmentation des contraintes génétiques, fonctionnelles, ontogéniques et/ou énergétiques

internes, permettant seulement certaines combinaisons de traits d'être réalisées à l'intérieur d'un groupe d'individus (Pigliucci 2003 ; Pigliucci & Preston 2004).

L'intégration phénotypique pourrait intervenir dans les processus d'ajustement des traits à l'environnement. Une forte intégration phénotypique au sein d'une espèce peut en effet refléter une plus faible variabilité phénotypique multi-variée, étant donné que plus un trait phénotypique est fortement lié à d'autres traits, plus sa gamme de variation est limitée (Gianoli & Palacio-Lopez 2009, Fig. 1a). Une forte intégration phénotypique peut aussi refléter une limitation d'une espèce dans la façon dont elle peut ajuster ses traits aux variations environnementales, étant donné que des traits intercorrélés répondent pareillement à un changement de l'environnement (Schlichting 1989b, Fig. 1b). De manière générale, une forte intégration phénotypique semble indiquer une faible capacité de réponse des traits aux variations de l'environnement (Schlichting 1989b).

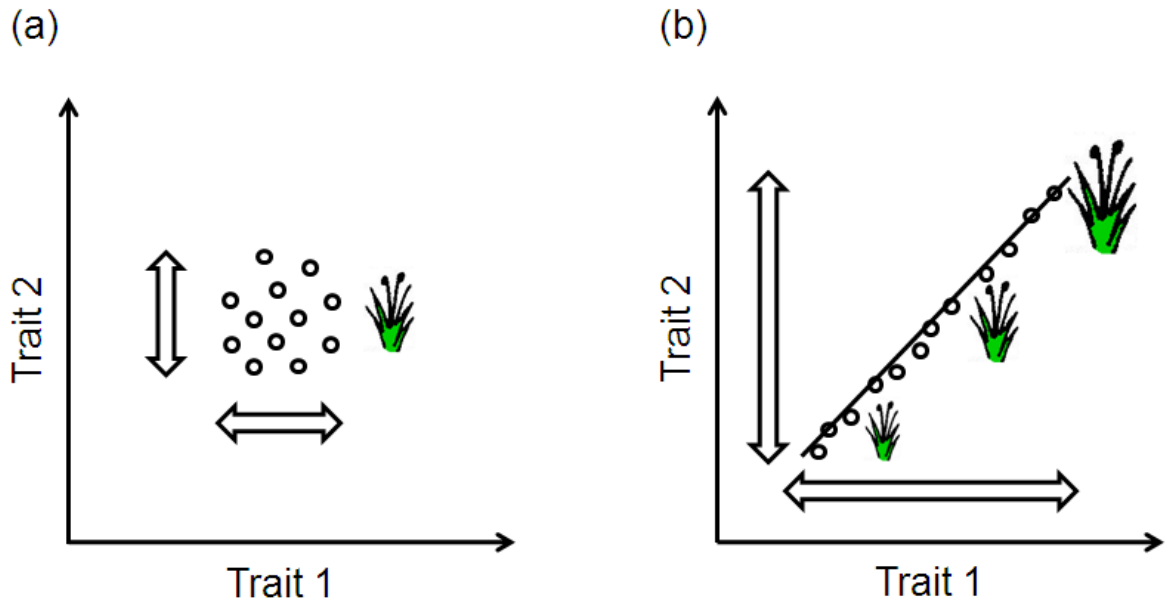


Figure 1 Schéma des deux explications alternatives pour une forte intégration phénotypique (i.e. force des corrélations entre les traits). Un point représente un individu de l'espèce considérée. Les traits 1 et 2 sont ici la hauteur et le diamètre des individus et leur variation est illustrée par les schémas de plantes. (a) Une forte intégration phénotypique à l'intérieur d'une espèce peut refléter une faible variabilité multivariée des traits (représentée ici par les flèches blanches). Quel que soit l'environnement occupé par les individus de l'espèce, ils expriment tous un phénotype très proche pour les traits considérés. (b) Une forte intégration phénotypique à l'intérieur d'une espèce peut refléter une limitation de l'espèce à réaliser seulement certaines combinaisons de traits (représentée ici par l'ajustement linéaire). Dans ce cas, la variabilité des traits peut être élevée. Des états intermédiaires entre (a) et (b) sont possibles. Les mêmes explications peuvent être appliquées à l'intégration entre des positions occupées par des individus le long de différents types de gradients environnementaux.

III.1.2. Définition de l'intégration environnementale

La littérature disponible décrit la distribution environnementale des espèces en termes de variabilité environnementale. De nombreuses recherches ont porté sur les concepts de *niche fondamentale* (i.e. l'ensemble des conditions environnementales et des ressources dans lesquelles les individus d'une population peuvent grandir et se reproduire avec succès, Hutchinson 1957) et de *niche réalisée* (i.e. l'ensemble des conditions environnementales occupées par une espèce en présence de compétiteurs et d'autres interactions biotiques, Hutchinson 1957). On parle de largeur de niche (*niche breadth*) ou de gamme écologique (*ecological breadth*) pour désigner l'amplitude écologique d'une espèce le long d'un ou plusieurs gradients environnementaux. L'étude des niches a notamment débouché sur l'idée que les espèces peuvent être plus ou moins spécialistes de certaines conditions environnementales. Les spécialistes maximisent leur performance (fitness) dans certains environnements et sont alors incapables d'occuper d'autres environnements (Levins 1968). Cette hypothèse implique l'existence de *trade-offs* (c'est-à-dire compromis ou corrélations négatives) entre les conditions environnementales occupées par une espèce.

La distribution écologique d'une espèce pourrait ainsi être contrainte par des corrélations entre les conditions abiotiques occupées par cette espèce. Nous définissons l'*intégration environnementale* comme une augmentation des contraintes génétiques, fonctionnelles, ontogéniques et/ou énergétiques internes, permettant à une espèce d'occuper seulement certaines combinaisons de conditions environnementales. Une forte intégration environnementale peut refléter une plus faible variabilité multivariée des conditions environnementales occupées (Fig. 1a), mais aussi de plus fortes corrélations (négatives ou positives) entre les conditions abiotiques occupées par l'espèce (Fig. 1b).

Tout comme l'intégration phénotypique, l'intégration environnementale pourrait intervenir dans les processus d'ajustement des traits à l'environnement. Une forte intégration

environnementale pourrait en effet contraindre une espèce à occuper une combinaison particulière de conditions environnementales et ainsi contraindre cette espèce à exprimer une combinaison particulière de traits. Une forte intégration environnementale pourrait ainsi influencer la valeur moyenne des traits, leur variabilité, mais aussi les corrélations entre les traits et l'environnement. En cela, elle pourrait également limiter la capacité de réponse des espèces à des variations de l'environnement, notamment si ces variations impliquent l'apparition de nouvelles combinaisons de facteurs environnementaux (Jackson & Overpeck 2000).

III.1.3. Intégration phénotypique et environnement

Plusieurs études ont montré qu'un renforcement de l'intégration phénotypique dépend de l'environnement abiotique occupé par les individus, et se produit notamment sous des conditions stressantes (Schlichting 1989a, b; Gianoli 2004; Waitt & Levin 1993; Pigliucci & Kolodynska, 2006). Cependant, ces études ont été principalement menées sur des plantes cultivées en serre, loin des contraintes environnementales multiples et combinées subies par les individus dans leur habitat naturel. De même, ces études cherchaient surtout à comprendre l'origine biologique et environnementale (conditions contrôlées, univariées) d'une forte intégration phénotypique. Les conséquences écologiques d'une forte intégration phénotypique n'ont été que très peu étudiées (Reich et al. 2003), tout comme son influence sur d'autres paramètres plus classiques tels que la moyenne et la variabilité des attributs de traits (Rapson & Maze 1994). De la même façon, à notre connaissance, l'influence de l'environnement biotique sur l'intégration phénotypique n'a jamais été testée. Le chapitre 1 de cette thèse a pour objectif d'étudier en détail l'intégration phénotypique chez une espèce dans son milieu naturel. Il se pose les questions suivantes : (i) Comment l'intégration phénotypique change-t-elle le long d'un gradient environnemental (biotique et abiotique) ? (ii) A quelle échelle

spatiale ce changement est-il important et doit-il donc être pris en compte dans les études sur les réponses phénotypiques des espèces aux conditions environnementales ? (iii) Un changement dans l'intégration phénotypique peut-il avoir un impact sur le changement de paramètres plus classiquement étudiés, comme la moyenne des attributs de traits ?

III.1.4. Rôle potentiel de l'intégration phénotypique et environnementale dans l'endémisme

Les causes de la distribution géographique réduite (i.e. endémisme) de certaines espèces ont été discutées depuis les prémices de l'écologie (de Candolle 1855), mais restent encore irrésolues de nos jours. Stebbins & Major (1965) ont émis l'hypothèse que les espèces endémiques seraient les vestiges de taxa dont les habitats spécialisés se seraient progressivement réduits au cours du temps (paléo-endémisme). D'autres auteurs suggèrent que les espèces endémiques ne seraient pas spécialistes de leurs habitats, mais auraient plutôt trouvé refuge dans des habitats stressants où la compétition interspécifique est plus faible (Gankin & Major 1964 ; Lavergne et al. 2003, 2004). Enfin, une dernière hypothèse suggère que les espèces endémiques seraient restreintes à des conditions environnementales particulières en raison d'une faible variabilité phénotypique (Rapson & Maze 1994 ; Sultan 2001). Ces trois hypothèses pour expliquer l'endémisme ont pu être démontrées pour certaines flores ou espèces endémiques (Gankin & Major 1964 ; Rapson & Maze 1994 ; Lavergne et al. 2003, 2004). Cependant, elles ne sont pas systématiquement validées (Fiedler 1987; Richards et al. 2005 ; Matesanz et al. 2009), ce qui laisse penser que d'autres processus pourraient intervenir dans l'endémisme.

Nous suggérons dans les paragraphes précédents qu'une forte intégration phénotypique et environnementale pourrait refléter une faible capacité de réponse phénotypique d'une espèce aux variations de l'environnement (Schlichting 1989b). Cela pourrait notamment avoir des implications sur la gamme écologique et géographique occupée par une espèce. Dans le

chapitre II de cette thèse, nous présentons l'intégration phénotypique et environnementale comme un nouveau facteur contribuant à l'endémisme. Nous émettons l'hypothèse qu'un fort niveau d'endémisme serait lié à (i) une forte intégration phénotypique (i.e. fortes corrélations entre les traits), (ii) une forte intégration environnementale (i.e. fortes corrélations entre les positions que l'espèce occupe le long de différents gradients environnementaux) et (iii) de fortes corrélations entre les traits et les environnements occupés.

III.2. La variabilité phénotypique réalisée au sein des clades

III.2.1. Définition de la variabilité phénotypique réalisée au sein des clades

La variabilité phénotypique au sein d'un clade constitue un cas particulier de variabilité interspécifique. De manière similaire à la variabilité intraspécifique (Albert et al. 2010a), elle peut être définie comme la gamme de valeurs d'un trait qui peut être réalisée entre différentes espèces, mais aussi la variabilité de ce qui est fonctionnellement expérimenté par les espèces d'un clade dans différentes conditions environnementales. Elle peut se mesurer comme une différence entre les moyennes du trait calculées chez les espèces du clade. Cette mesure simple de la variabilité des traits au sein des clades ne prend pas en compte les relations phylogénétiques entre les clades et à l'intérieur des clades. Elle ne prend pas non plus en compte l'âge du clade. C'est une mesure de diversité fonctionnelle réalisée actuellement au sein d'un clade dans un environnement donné. Nous savons que les clades au sein d'une région présentent, à l'époque actuelle, des niveaux différents de variabilité phénotypique réalisée, comme il est indiqué par de nombreux exemples dans chaque flore ou faune (Jäger & Werner 2002). Cette variation est un aspect majeur, mais très peu étudié, de la biodiversité.

Le niveau de variabilité phénotypique réalisée au sein d'un clade dans une région donnée pourrait refléter différents processus (Fig. 2). La variabilité phénotypique réalisée au sein des clades peut dépendre de leur âge (Ackerly & Nyffeler 2004). Les clades les plus âgés auraient

disposé de plus de temps pour se diversifier et présenteraient donc actuellement une plus grande variabilité réalisée (Fig. 2a). Mais le niveau de variabilité réalisée dans un clade peut aussi dépendre de la position occupée par ce clade le long des gradients environnementaux.

III.2.2. Variabilité phénotypique réalisée au sein des clades et environnement abiotique

Selon l'hypothèse du conservatisme phylogénétique des niches (i.e. les niches sont moins variables dans les clades que ce qui est attendu aléatoirement), les clades occuperaient des environnements abiotiques qui leur sont spécifiques (Prinzing et al. 2001 ; Wiens & Graham 2005). Existe-t-il un lien entre la variabilité phénotypique réalisée au sein d'un clade et la position environnementale abiotique qu'il occupe ?

► *Opportunités environnementales inhérentes à certains environnements pour les espèces* (Fig. 2b): certains environnements présenteraient les conditions abiotiques et biotiques favorables au rassemblement d'espèces très différentes dans leurs traits (Stevens et al. 2003; Ackerly & Cornwell 2007). Ces environnements favoriseraient l'établissement et le maintien de hauts niveaux de diversité de traits dans le pool d'espèces qui les occupent. Cela serait indépendant du taux de diversification des traits dans les clades, mais les clades étant distribués inégalement entre les environnements pourraient refléter ces processus environnementaux (Prinzing et al. 2001 ; Wiens & Graham 2005).

► *Opportunités environnementales inhérentes aux espèces appartenant à un même clade* (Fig. 2c): certains environnements présenteraient les conditions abiotiques et biotiques favorables au rassemblement de clades dont les espèces sont très différentes dans leurs traits (sur le niveau des communautés : Helmus et al. 2007a ; Gomez et al. 2010). Un environnement abiotique donné pourrait par exemple contenir un grand nombre de compétiteurs du même clade ou pourrait contenir les phytophages ou pollinisateurs spécialisés d'un clade. Ces environnements favoriseraient l'établissement et le maintien de hauts niveaux

de variabilité de traits dans les clades qui les occupent, sans augmenter la variabilité des traits dans le pool d'espèces correspondant.

Le chapitre III de cette thèse a pour objectif de discriminer les trois hypothèses décrites ci-dessus. Plus précisément, ce chapitre pose les questions suivantes : (i) La variabilité phénotypique réalisée au sein des clades dépend-elle de leur âge ? (ii) La variabilité phénotypique réalisée au sein des clades dépend-elle de l'environnement abiotique occupé ? (iii) La variabilité phénotypique réalisée au sein des clades reflète-t-elle la variabilité phénotypique au sein du pool d'espèces dans l'environnement abiotique? (iv) La variabilité phénotypique réalisée au sein des clades dans un environnement abiotique donné résulte-t-elle d'une forte intégration entre le phénotype et l'environnement abiotique ?

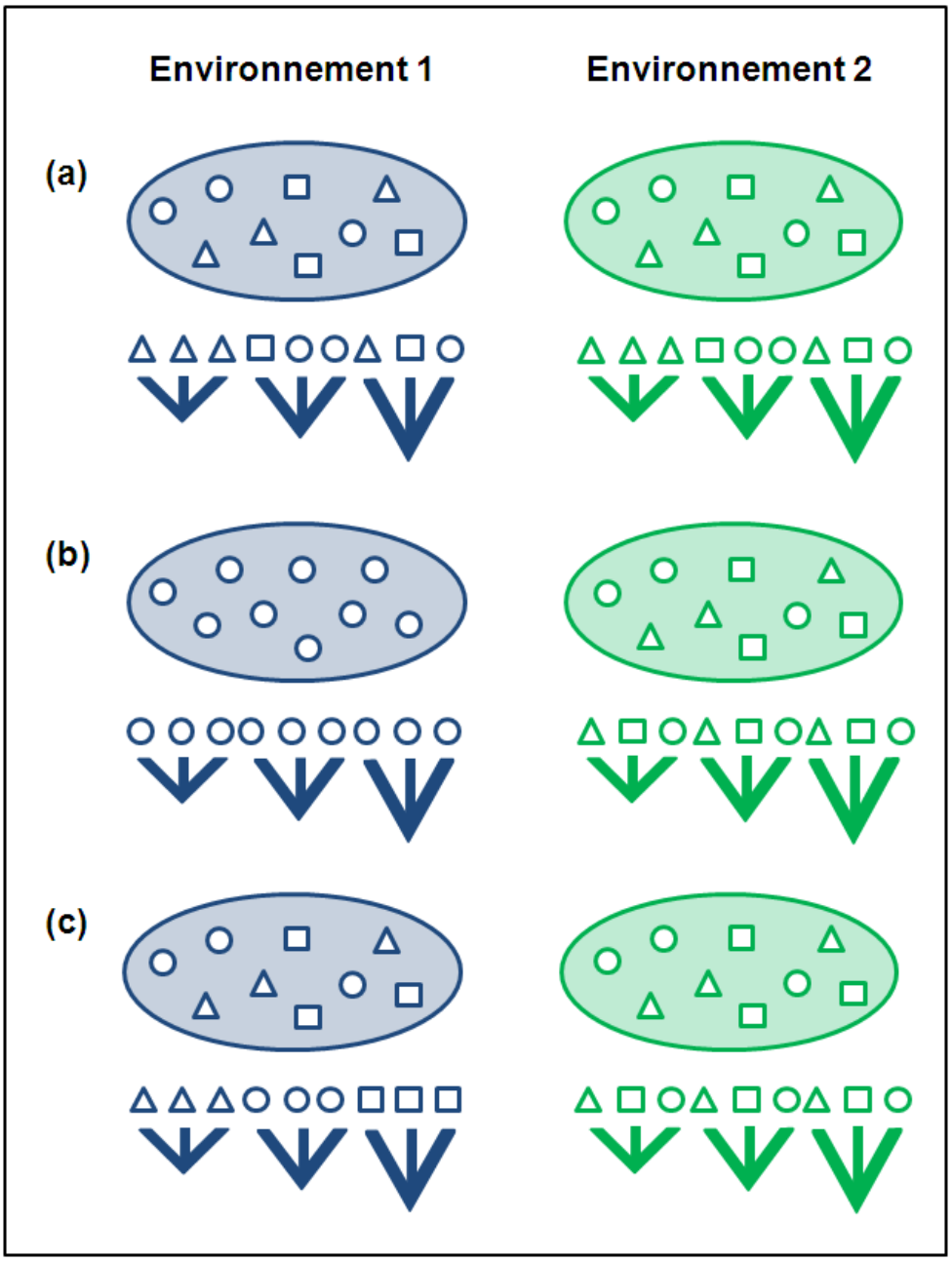


Figure 2 Schémas des différents processus à l'origine de la variabilité phénotypique réalisée au sein des clades. Les ellipses respectivement bleues ou vertes représentent deux environnements différents. Les petits cercles, triangles et carrés blancs représentent différents attributs du même trait pour neuf espèces différentes occupant les environnements 1 et 2. Dans chaque environnement, les espèces sont réparties dans trois clades différents (trois espèces par clade). Dans le cas (a), la variabilité des traits réalisée au sein des clades est totalement indépendante de l'environnement et dépend uniquement de l'âge du clade. Dans le cas (b), la variabilité des traits réalisée au sein des clades ne dépend pas de l'âge des clades ni de leur position phylogénétique. Elle dépend de l'environnement et reflète la variabilité au sein du pool d'espèces. Dans le cas (c), la variabilité des traits réalisée au sein des clades ne dépend pas de l'âge des clades. Elle varie entre les environnements, mais ne reflète pas la variabilité au sein du pool d'espèces. Elle dépend à la fois de l'environnement et des positions phylogénétiques.

III.2.3. Variabilité phénotypique réalisée au sein des clades et interactions biotiques

La coexistence des espèces est considérée comme particulièrement labile localement (par exemple, au sein d'une communauté, Rosenzweig 1995 ; Ricklefs 2008). Cependant, serait-il possible qu'à l'échelle d'une région entière, certaines espèces coexistent avec beaucoup d'espèces tandis que d'autres coexistent avec peu d'espèces ? De telles différences pourraient-elles dépendre de l'appartenance des espèces à des clades particuliers ?

Plusieurs raisons nous incitent à penser que le niveau de coexistence des espèces pourrait être conservé dans les clades à l'échelle d'une région : premièrement, la richesse spécifique locale se répartirait différemment dans l'environnement abiotique (Ewald 2003), tout comme les clades (conservatisme phylogénétique des niches, Prinzing et al. 2001 ; Wiens & Graham 2005). Ainsi, le nombre d'espèces qui coexistent localement pourrait varier entre les différents environnements abiotiques et entre les clades. La perturbation et la compétition interspécifique sont d'autres facteurs influençant la coexistence locale des espèces (Goldberg & Barton 1992 ; Shea et al 2004). Le nombre d'espèces qui coexistent localement pourrait aussi varier entre les clades, si ces différents clades occupent des environnements plus ou moins perturbés ou présentent des capacités compétitives différentes.

S'il s'avère que le niveau de coexistence interspécifique est conservé à l'intérieur des clades, nous pouvons alors faire l'hypothèse d'un lien entre la variabilité phénotypique réalisée au sein d'un clade et le nombre d'espèces en coexistence au sein de ce clade. Cette hypothèse peut être envisagée à travers deux concepts :

► *Règles d'assemblages des communautés* : les interactions entre les espèces influenceraient leurs traits. Par exemple, la compétition peut jouer un rôle de filtre sur les traits des espèces végétales (Navas & Violle 2009). Ces effets « filtre » sont notamment influencés par les relations phylogénétiques entre les espèces (Mayfield & Levine 2010). D'autres exemples indiquent un effet local des ennemis naturels (Diaz et al. 2007), ou des

interactions positives (par exemple, mutualisme ou facilitation, Gross et al. 2009) avec d'autres espèces sur les traits. Ces interactions peuvent être spécifiques à certains clades (DiMichele et al. 2004) et pourraient alors uniquement influencer la variabilité des traits au sein de ces clades.

► *Diversification des traits* : la coexistence interspécifique influence la diversification des traits. La compétition entre espèces induit des déplacements de caractères (Bridle & Vines 2006 ; Pfennig 2009). Les interactions plantes-phytophages (Futuyama & Agrawal 2009) et les interactions mutualistes (Thompson 2005) peuvent contribuer à la diversification des traits au sein des clades par des phénomènes de co-évolution.

Le chapitre IV de cette thèse a pour objectif de comparer les niveaux de coexistence interspécifique entre les clades et de quantifier le rôle de ces interactions biotiques potentielles sur la variabilité phénotypique réalisée au sein des clades. Nous posons les questions suivantes : (i) Les clades diffèrent-ils dans leur degré de coexistence avec d'autres espèces (i.e. le niveau de coexistence des espèces est-il conservé au sein des clades) ? (ii) Le degré de coexistence des espèces d'un clade dépend-il de l'environnement abiotique occupé, de la compétitivité des espèces, de leur rudéralité, et enfin de l'âge du clade ? (iii) Une grande variabilité des attributs d'un trait au sein d'un clade est-elle le résultat d'une forte coexistence des espèces au sein de ce clade ?

III.2.4. Implication d'une relation entre la variabilité phénotypique réalisée au sein des clades et l'environnement abiotique et biotique

Si les conditions abiotiques et biotiques jouent un rôle important dans l'émergence et le maintien de niveaux particuliers de variabilité phénotypique au sein des clades, cela pourrait avoir diverses implications :

► *Diversité fonctionnelle et phylogénétique des communautés* : la relation entre le nombre de clades dans une communauté (ou plus généralement sa diversité phylogénétique) et le nombre d'attributs de traits dans cette communauté serait dépendante du contexte abiotique et biotique. Cela pourrait remettre en question l'hypothèse largement répandue que la diversité phylogénétique des communautés peut être utilisée comme un simple proxy de la variabilité des attributs de traits (Webb *et al.* 2002; mais voir aussi Prinzing *et al.* 2008 ou Swenson & Enquist 2009).

► *Conservation de la diversité fonctionnelle des clades* : la diversité fonctionnelle au sein des clades pourrait subir les conséquences des actions anthropiques. Par exemple, l'érosion de la diversité spécifique modifie les conditions biotiques du milieu, alors que le changement climatique (Midgley & Thuiller 2007 ; Feehan *et al.* 2008) et l'augmentation des pollutions (Tilman 2002) pourraient altérer les conditions abiotiques. Les conséquences pourraient se généraliser aux espèces en interaction avec les plantes, comme les pollinisateurs ou les phytophages spécifiques de certains clades (Johnson 2010).

► *Homogénéisation évolutive de la flore* : les activités humaines peuvent perturber davantage certaines espèces caractérisées par certains traits. Par exemple, les plantes de petite taille et produisant de petites graines semblent davantage soumises à l'extinction dans les zones urbaniséees (Williams et al. 2010). Dans des environnements (abiotiques et biotiques) où les clades sont particulièrement pauvres dans leurs traits, ces activités humaines pourraient induire la disparition de clades entiers et donc une homogénéisation évolutive de la flore dans ces environnements.

Ces implications sont discutées plus précisément au sein des chapitres 3 et 4, mais ne seront pas testées dans la thèse.

IV. Systèmes biologiques étudiés

IV.1. Les espèces végétales des îles subantarctiques

IV.1.1. Biogéographie

La région subantarctique comprend six groupes d'îles s'étendant entre les latitudes 46° et 55°S (Van der Putten et al. 2010). Sur la base de la composition floristique des différentes îles subantarctiques, la région peut être divisée en trois provinces (Fig. 3) : la Province Sud de l'Océan Atlantique qui comporte la Géorgie du Sud, la Province Sud de l'Océan Pacifique qui comporte l'Ile Macquarie et enfin la Province Sud de l'Océan Indien qui comporte les Iles Marion et Prince Edward, les Iles Crozet, les Iles Kerguelen et le groupe de l'Ile Heard (Skottsberg 1960 ; Smith 1984).

Les îles subantarctiques sont d'origine volcanique, sauf la Géorgie du Sud qui est d'origine continentale, et l'Ile Macquarie qui est d'origine tectonique. La Géorgie du Sud est l'île la plus ancienne (120 millions d'années). Les Iles Kerguelen et l'Ile Heard ont émergé au début du Tertiaire (40 millions d'années) (Nicolaysen et al. 2000). Les restes fossiles nous montrent qu'à cette époque les Iles Kerguelen étaient couvertes de forêts tempérées (Philippe et al. 1998). Cette végétation a connu un maximum autour de -20 millions d'années et a été presque entièrement éliminée par les glaciations subséquentes au Quaternaire (d'environ -2,7 millions d'années à aujourd'hui) (Giret et Nougier 1989). Les Iles Crozet ont émergé plus récemment (8 millions d'années). Toutes les autres îles subantarctiques ont émergé pendant le Quaternaire, il y a moins de 600 000 ans.

Différentes théories ont été émises pour expliquer la biogéographie de la flore subantarctique. La présence d'espèces endémiques au milieu d'une flore autochtone circumpolaire a d'abord fait suggérer l'existence de deux étapes bien distinctes dans l'évolution de la flore australe (Hooker 1847 ; Werth 1911). Les espèces endémiques actuelles seraient des reliques de l'ère tertiaire, ayant survécu aux glaciations dans des refuges non

entièrement glacés, tels que des nunataks. A l'inverse, les espèces autochtones circumpolaires devraient leur distribution actuelle à des migrations circum-antarctiques survenues après les glaciations, au Quaternaire. L'existence de trois provinces phytogéographiques dans la région subantarctique soutenait fortement cette double théorie (Skottsberg 1960). La première hypothèse a été remise en cause par Wace (1960) qui suggérait que la végétation tertiaire aurait complètement disparu pendant les périodes glaciaires et que l'intégralité de la flore actuelle résulterait d'une colonisation post-glaciaire des espèces à partir des continents plus tempérés de l'hémisphère austral. Cependant, la découverte ultérieure de pollen de deux espèces endémiques de la Province Sud de l'océan Indien (*Pringlea antiscorbutica* et *Lyallia kerguelensis*) dans des carottes géologiques de la dernière période glaciaire a constitué une première preuve possible de leur origine tertiaire (Young & Shofield 1973). De nouvelles données paléobotaniques supportent cette hypothèse (Van der Putten et al. 2010). La plupart des espèces de la flore actuelle ont en effet été trouvées dans les sédiments organiques accumulés sur les îles subantarctiques à la fin du dernier maximum glaciaire, indiquant l'absence d'importants événements d'immigration post-glaciaire depuis les continents plus tempérés.

IV.1.2. Pourquoi travailler sur les espèces végétales des Îles Crozet et Kerguelen ?

Les chapitres I et II de la thèse s'intéressent plus particulièrement aux îles des Terres Australes et Antarctiques Françaises, notamment les Îles Crozet (Île de la Possession à 46° 24′ 41″ S de latitude et 51° 45′ 22″ E de longitude) et les Îles Kerguelen (49° 20' 57'' S de latitude et 70° 13' 07'' E de longitude à Port-aux-Français). Ce système est d'un intérêt particulier pour la thèse en raison de trois critères principaux :

► Ces îles portent de forts gradients abiotiques, notamment l'un des gradients altitudinaux de température les plus importants au monde avec une diminution moyenne de 0,8°C par 100m aux Îles Kerguelen (Hennion et al. 2006a).

► La flore autochtone actuelle des îles Crozet et Kerguelen est assez pauvre en espèces et relativement peu perturbée par les activités humaines (Smith 1984; Frenot et al. 2001). Les phanérogames autochtones sont recensées au nombre de 17 espèces sur l'Île de la Possession (Îles Crozet) et de 22 espèces sur les Îles Kerguelen. Le nombre d'espèces de plantes vasculaires introduites est plus important : 101 sur les Îles Crozet et 86 sur les Îles Kerguelen (Frenot et al. 2001). Ces espèces auraient été introduites depuis la fréquentation des îles par l'Homme, au cours des deux derniers siècles (Frenot et al. 2005).

► Les phanérogames des Îles Crozet et Kerguelen présentent des amplitudes de distribution géographique diverses. La Province Sud de l'Océan Indien comporte 6 espèces endémiques (*Lyallia kerguelensis*, *Colobanthus kerguelensis*, *Poa cookii*, *Poa kerguelensis*, *Pringlea antiscorbutica* et *Ranunculus moseleyi*), dont l'une (*Lyallia kerguelensis*) est strictement endémique des Îles Kerguelen. *Poa cookii* est également présente sur l'Île Macquarie (Edgar 1986). Les autres espèces autochtones ont une distribution plus large. On distingue des espèces restreintes à la couronne circumpolaire (par exemple, *Deschampsia antarctica*, *Festuca contracta, Ranunculus biternatus*), d'autres s'étendant vers l'Amérique du Sud (par exemple, *Acaena magellanica*), ou même des espèces cosmopolites (par exemple, *Montia fontana*) (Lourteig & Cour 1963 ; Walton 1979 ; Edgar 1986 ; Frenot et al. 2001 ; Van der Putten et al. 2010).

Figure 3 Vue de l'hémisphère sud montrant la Zone du Front Polaire et la subdivision du biome Antarctique en zones Continentale, Maritime et Subantarctique. La zone Subantarctique peut être divisée en trois provinces (ellipses en pointillés), i.e. la Province Sud de l'Océan Atlantique qui comporte la Géorgie du Sud, la Province Sud de l'Océan Pacifique qui comporte l'Île Macquarie et enfin la Province Sud de l'Océan Indien qui comporte les Îles Marion et Prince Edward, les Îles Crozet, les Îles Kerguelen et le groupe de l'Île Heard. D'après Van der Putten et al. (2010).

1.4.1.3. Les espèces végétales étudiées dans la thèse

Le chapitre I de la thèse est consacré au Chou de Kerguelen (*Pringlea antiscorbutica* R. Br., Fig. 4j). Cette espèce est endémique de la Province Sud de l'Océan Indien (Îles Marion et Prince Edward, Îles Crozet, Îles Kerguelen, Îles Heard et McDonald, Fig. 2) (Hennion & Walton 1997a). Cette crucifère était une espèce très commune à Kerguelen avant l'introduction du lapin (Hooker 1847 ; Aubert de la Rüe 1964). Malgré l'impact du lapin, elle couvre encore une large gamme d'habitats du littoral jusqu'à environ 1000 m d'altitude. Elle colonise de préférence les zones humides bien drainées (Hennion & Walton 1997a). *P. antiscorbutica* est une plante pérenne à reproduction uniquement sexuée, dont les individus matures produisent un grand nombre de graines chaque année (Hennion & Walton 1997b; Schermann-Legionnet et al. 2007). C'est une espèce à pollinisation auto-compatible, essentiellement autogame, mais vraisemblablement aussi dispersée par le vent (Schermann-Legionnet et al. 2007). La dispersion des graines entre les îles du Golfe du Morbihan par flottaison de hampes florales dans l'eau de mer a été observée à Kerguelen (Chapuis et al. 2004), mais la dispersion au sol par l'eau douce ou le vent n'excède pas quelques mètres (Hennion & Walton 1997a; Schermann-Legionnet et al. 2007). La déhiscence des fruits se produit en janvier dans les populations les plus précoces de basse altitude, mais pas avant mars à haute altitude.

Le chapitre II de la thèse s'intéresse, en plus de *P. antiscorbutica*, à 14 espèces de phanérogames présentes sur les Îles Kerguelen (Fig. 4). Ces espèces ont été principalement choisies en raison de la gamme de distribution géographique qu'elles représentent, de l'endémisme de la Province Sud de l'Océan Indien autour des Îles Kerguelen jusqu'à une répartition mondiale (Fig. 5, Lourteig & Cour 1963 ; Walton 1979 ; Edgar 1986 ; Frenot et al. 2001 ; Van der Putten et al. 2010). Les 14 espèces appartiennent à sept familles différentes d'Angiospermes (Angiosperm Phylogeny Group III, Bremer et al. 2009). Quatre d'entre elles

sont d'origine introduite récente, moins de deux cents ans, sur les Îles Kerguelen (Frenot et al. 2001). Leur forme de croissance, leur mode de dispersion (sexué, végétatif), ainsi que leur mode de reproduction ont pu être déterminés à partir de la littérature (Chastain 1958; Cour 1958; Tallowin & Smith 1977; Convey 1996; Hennion & Walton 1997a; Durka 2002; Pakeman et al. 2002; Robinson et al. 2003; Chapuis et al. 2004 ; Schermann et al. 2007; Kleyer et al. 2008).

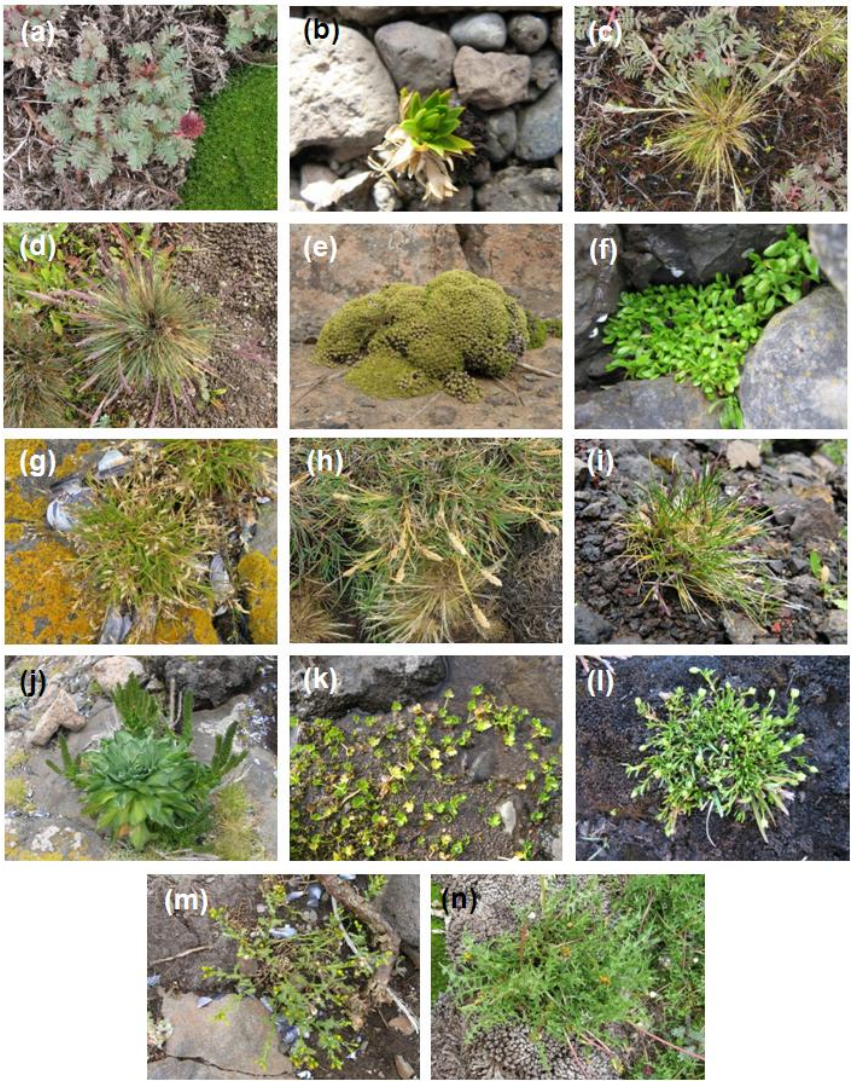
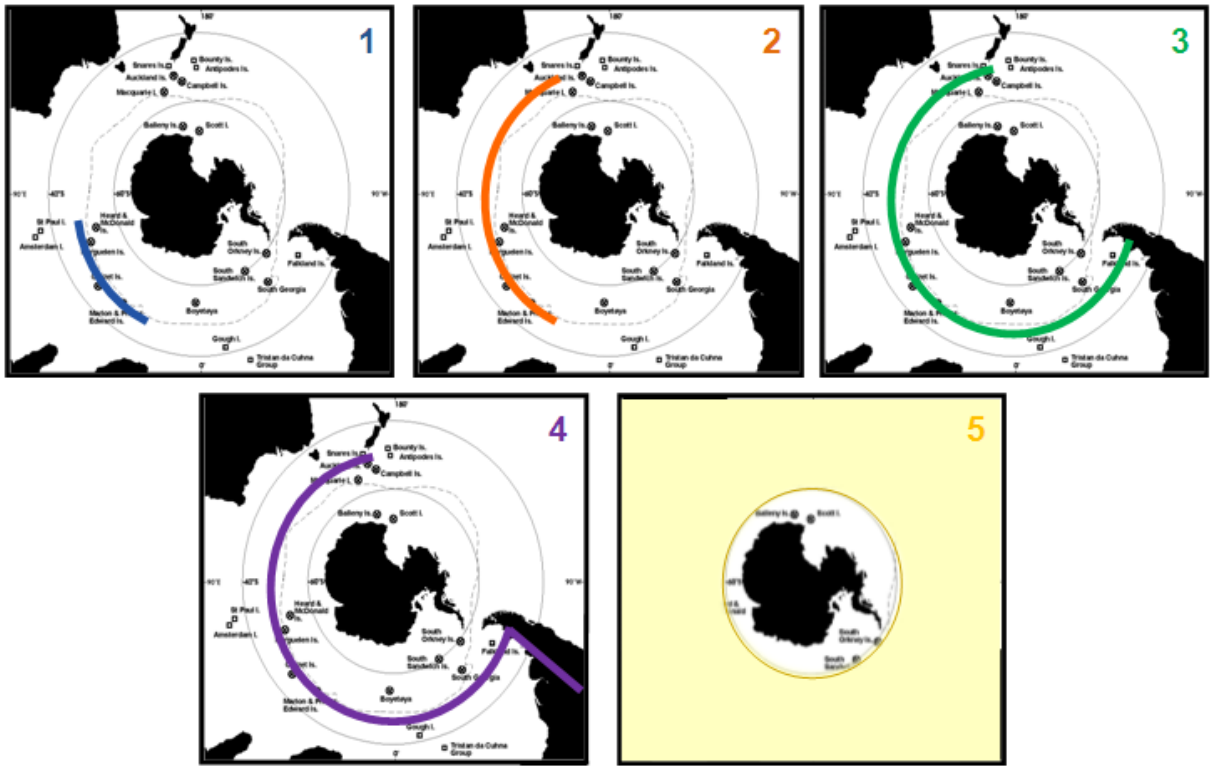


Figure 4 Présentation des 14 espèces de phanérogames étudiées dans la thèse (photos : Marie Hermant). (a) *Acaena magellanica*, (b) *Colobanthus kerguelensis*, (c) *Deschampsia antarctica*, (d) *Festuca contracta*, (e) *Lyallia kerguelensis*, (f) *Montia Fontana*, (g) *Poa annua*, (h) *Poa cookii*, (i) *Poa kerguelensis*, (j) *Pringlea antiscorbutica*, (k) *Ranunculus biternatus*, (l) *Sagina procumbens*, (m) *Senecio vulgaris*, (n) *Taraxacum erythrospermum*.



Niveau d'endémisme	Distribution géographique
1	Endémique des Îles Kerguelen ou de la Province Sud de l'Océan Indien
2	Endémique d'îles de la Province Sud de l'Océan Indien et de l'Île Macquarie
3	Circumpolaire australe
4	Australe
5	Cosmopolite

Figure 5 Classification des 14 espèces en fonction de leur distribution géographique (Lourteig & Cour 1963 ; Walton 1979 ; Edgar 1986 ; Frenot et al. 2001 ; Van der Putten et al. 2010).

IV.1.4. Conditions environnementales dans les îles Crozet et Kerguelen

IV.1.4.1. Les habitats des îles Crozet et Kerguelen

Les Îles Crozet et Kerguelen sont caractérisées par un grand nombre de types d'habitats et de végétation, qui ont été particulièrement bien décrits par Chastain (1958), Smith (1984) et plus récemment Lebouvier et al. (2009, non publié). Ces habitats sont essentiellement déterminés par l'exposition au vent et le degré de drainage des sols (Hennion 1992). Nous décrirons ici rapidement les principaux habitats que nous avons observés à Crozet et à Kerguelen.

► Les prairies à mégaherbes, ou *Herbfield* sont caractéristiques des zones humides et protégées de basse altitude. Elles comportent une végétation dense et fermée, dominée par des plantes pérennes (Hennion et al. 2006a). La compétition intra- et interspécifique y est certainement plus forte qu'à haute altitude. Cette catégorie recouvre différents habitats. Nous avons notamment observé les *pelouses littorales* (Fig. 6a), qui sont principalement restreintes à la zone de rivage des îles et caractérisées par des sols salés et enrichis. Nous avons également travaillé sur la prairie à *Azorella Selago, Pringlea antiscorbutica et Festuca contracta* (Fig. 6b). C'est l'habitat le plus varié d'un point de vue floristique et son organisation sociologique est complexe (Chastain 1958). Cet habitat est aujourd'hui limité aux îles protégées des herbivores introduits (par exemple, l'île Australia). Enfin, la *lande ou prairie à Acaena magellanica* (Fig. 6c) occupe les plaines tourbeuses littorales et intérieures, où abondent les herbivores introduits. Principalement dominée par *Acaena magellanica*, cette lande couvre une zone très importante, presque tout l'est de la Péninsule Courbet.

► Les *Fell-field* ou « champs d'altitude » (Fig. 6d) se trouvent sur des plateaux exposés et des crêtes, dans des sites caractérisés par des conditions abiotiques très contraignantes pour les organismes (vents violents, faibles températures, faible rétention en eau, faible teneur en matière organique, instabilité du sol et érosion active de la surface du sol). Plus souvent trouvés en haute altitude, ces habitats existent aussi à basse altitude dans des zones très

exposées aux vents dominants. La végétation est ouverte et les plantes présentent des morphotypes caractéristiques des conditions contraignantes de l'environnement (par exemple, forme aplatie ou en coussin, Chastain 1958).

IV.1.4.2. Changement climatique dans les îles Crozet et Kerguelen

Les conditions climatiques des îles subantarctiques françaises sont caractérisées par de fortes précipitations et de faibles amplitudes thermiques saisonnières. Les moyennes annuelles de température sont plus froides à Kerguelen (4,6°C sur la période 1951-2008) qu'à Crozet (5,3°C) (Lebouvier & Frenot 2007). Les moyennes annuelles de précipitations sont par contre plus élevées à Crozet (2400 mm) que dans l'est des Îles Kerguelen où est mené l'essentiel des programmes de recherche (760 mm, Lebouvier & Frenot 2007).

Le changement climatique dans les îles subantarctiques françaises a été étudié à partir de données météorologiques enregistrées depuis 1950 à Port-aux-Français (à l'est des Îles Kerguelen). Il se traduit par une augmentation de 1,3°C des moyennes annuelles de températures et une réduction d'environ 700 mm des moyennes annuelles de précipitations (Frenot et al. 2006). Si ces changements semblent faibles, ils restent néanmoins relativement forts pour des espèces ectothermes habituées à des conditions climatiques froides et très tamponnées.

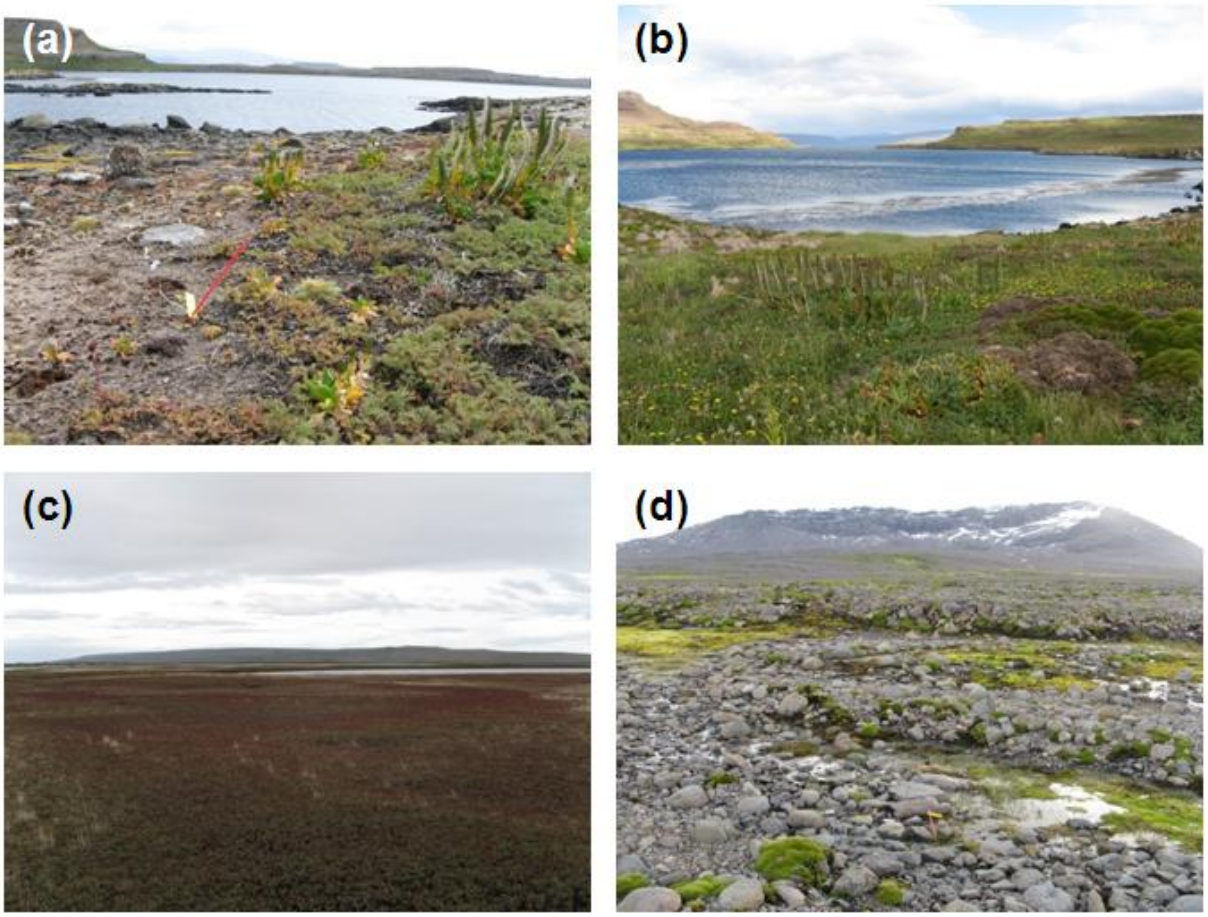


Figure 6 Exemples d'habitats rencontrés pendant notre échantillonnage sur les Îles Kerguelen. (a) Pelouse littorale sur l'île Australia, (b) Prairie à *Azorella Selago*, *Pringlea antiscorbutica* et *Festuca contracta* sur l'île Australia, (c) Landes ou prairie à *Acaena magellanica* sur l'île Guillou, (d) Fellfield au Mont Crozier, Val Studer.

IV.2. Les genres d'Angiospermes de l'Europe Centrale

IV.2.1. Pourquoi travailler sur les genres d'Angiospermes de l'Europe Centrale ?

L'objectif des chapitres III et IV est de tester les rôles des environnements abiotiques et biotiques dans la variabilité phénotypique réalisée au sein des clades. L'un des intérêts majeurs est de tester cette hypothèse à l'échelle d'une région entière. Pour cela, nous avons besoin :

► D'une région du monde pour laquelle la description des traits et de l'environnement abiotique et biotique d'un grand nombre d'espèces de plantes est facilement disponible. L'Europe Centrale remplit parfaitement ce critère. On dispose pour cette région de grandes connaissances naturalistes sur les traits d'histoire de vie des espèces végétales, sur leur environnement et sur leur coexistence.

► De travailler sur plusieurs traits. En Europe Centrale, les connaissances sur de nombreux traits d'histoire de vie des espèces végétales ont récemment été compilées dans plusieurs bases de données, dont la plus vaste est BiolFlor (Klotz *et al.* 2002).

► De mesurer la variabilité des traits réalisée au sein du plus grand nombre possible de clades des taxons majeurs de la région. La base de données BiolFlor décrit les traits de 838 genres et 131 familles d'Angiospermes de l'Europe Centrale (Klotz *et al.* 2002).

► De mesurer la variabilité des traits réalisée dans les différents environnements abiotiques et biotiques sur un niveau taxonomique approprié. Les genres d'Angiospermes sont connus pour occuper différentes conditions abiotiques (par exemple, Prinzing et al. 2001) et les naturalistes observent que certains genres sont plus variables dans leurs traits que d'autres (Jäger & Werner 2002). Les genres monophylétiques (bien que correspondant à un niveau de classification relativement arbitraire) constituent donc une unité exploitable dans les analyses macro-écologiques. De plus, le niveau genre intègre les événements de diversification qui se

sont produits dans une fenêtre de temps limitée, et est lui-même classé dans des familles, ce qui permet de tester la cohérence des patterns à l'intérieur des familles.

► De comparer chez ces clades les niveaux de la variabilité réalisée des traits en fonction du niveau de coexistence de leurs espèces avec d'autres espèces. La coexistence d'un grand nombre d'espèces végétales des Pays-Bas a été mesurée sur 350 000 relevés et les valeurs de ce paramètre sont disponibles dans la base de données SynBioSys (Hennekens & Schaminée 2001).

► De comparer les niveaux de la variabilité réalisée des traits entre des clades occupant des positions intermédiaires et des clades occupant des positions extrêmes le long de plusieurs gradients abiotiques. Les connaissances sur l'environnement abiotique occupé par la majorité des espèces d'Angiospermes de l'Europe Centrale sont essentiellement disponibles au sein de systèmes de classification tels que les valeurs indicatrices d'Ellenberg (Ellenberg 1992).

IV.2.2. Les traits d'histoire de vie

La base de données BiolFlor compile les informations de la littérature sur 60 traits d'histoire de vie de la flore de l'Europe Centrale (Klotz *et al.* 2002). Les 3660 espèces décrites dans cette base appartiennent à 838 genres et 131 familles d'Angiospermes. La nomenclature et la classification de ces espèces suit principalement Jäger & Werner (2002) et le *Angiosperm Phylogeny Group III* (Bremer *et al.* 2009). Parmi les 60 traits disponibles, nous avons choisi de travailler sur les traits connus pour répondre aux changements environnementaux (Smith et al. 1997). Nous avons exclu les traits qui varient fortement au sein des espèces (tels que la taille des plantes), ceux qui manquaient pour un grand nombre d'espèces (tels que la surface spécifique foliaire ou SLA) ou ceux qui étaient codés sur une échelle catégorielle (rendant le calcul de la variabilité des traits difficile et incohérent en comparaison avec des traits continus ou ordonnés). Nous avons retenu le début de la floraison, la durée de la floraison, la durée de

vie des plantes, la masse des graines, la tolérance au stress et le type de reproduction. Ces traits sont des traits d'histoire de vie classiques, sauf la tolérance au stress qui est plutôt un indicateur des performances écologiques de la plante et dépend de la réponse coordonnée de multiples traits d'histoire de vie aux facteurs environnementaux (Violle *et al.* 2007).

IV.2.3. Les données de coexistence

Le réseau SynBioSys est un réseau hollandais basé à Alterra (Green World Institute, Wageningen) et dont le nom complet est 'Syntaxonomisch Biologisch Systeem'. Il est composé de plus de 350 000 relevés phytosociologiques établis aux Pays-Bas. Ces mesures ont été compilées dans une base de données exploitable à partir du logiciel TURBOVEG (Hennekens & Schaminée 2001). Cette base de données fournit des informations sur la composition floristique et la distribution géographique des communautés de plantes et permet notamment des mesures de coexistence des espèces.

IV.2.4. Conditions environnementales en Europe Centrale

Le système de classification d'Ellenberg décrit les environnements occupés par la majorité des espèces d'Angiospermes de l'Europe Centrale (Ellenberg 1992). Ce système donne la position des espèces le long de six gradients abiotiques: luminosité, température, continentalité, humidité du sol, pH du sol et contenu du sol en composés azotés. Les valeurs indicatrices d'Ellenberg sont des estimateurs de l'habitat optimal de chaque espèce et sont exprimées sur des échelles ordinales comprenant 9 à 12 rangs.

La mesure *in situ* de l'environnement abiotique occupé par les espèces serait évidemment préférable à un système de classification fondé sur l'estimation d'experts, tel que celui d'Ellenberg. Néanmoins, nous estimons que l'utilisation des valeurs indicatrices d'Ellenberg valable en Europe Centrale pour les raisons suivantes :

► Pour un nombre élevé d'espèces et de genres de l'Europe Centrale, des mesures *in situ* de l'environnement ne sont pas disponibles. En l'absence de mesures plus précises, la plupart des régions du monde se voient d'ailleurs contraintes de développer des systèmes de classification proches de celui d'Ellenberg, comme par exemple le BEC (British Columbia Ecological Classification, Britton et al. 1996) ou encore les *Wetland Indicator Status* du United States Department of Agriculture (USDA, NRCS 2010, http://plants.usda.gov) en Amérique du Nord.

► De fortes corrélations entre les valeurs indicatrices d'Ellenberg et des mesures *in situ* de l'environnement ont été démontrées (Hill & Carey 1997; Diekmann 2003; Ozinga *et al.*, 2004). Ces études valident l'utilisation des valeurs d'Ellenberg comme des variables environnementales.

► L'utilisation des valeurs indicatrices d'Ellenberg comme variables continues se révèle statistiquement fiable (Ter Braak & Gremmen 1987).

Une solution alternative à l'utilisation de systèmes de classification serait de prédire la distribution climatique des espèces à partir de modèles de distribution des espèces (Guisan & Zimmermann 2000). Cependant, une telle construction n'est pas encore possible pour beaucoup d'espèces et de genres d'Angiospermes en Europe Centrale. De plus, ces modèles comportent leurs propres limites. Par exemple, la distribution des espèces n'est souvent prédite qu'à partir de facteurs climatiques (par exemple, température ou précipitations, Guisan & Zimmermann 2000), parfois combinés avec des données d'occupation biophysique des sols (Thuiller et al. 2004b ; Araújo et al. 2005). Les modèles prennent rarement en compte d'autres paramètres écologiques majeurs influençant la distribution des espèces, comme les propriétés du sol (par exemple, la quantité de ressources, Hanspach et al. 2009). Les valeurs d'Ellenberg donnent des indications sur de tels paramètres écologiques en décrivant la tolérance des espèces en termes de luminosité, humidité du sol, pH du sol et contenu du sol en azote. Ces

valeurs permettent une estimation multivariée de l'habitat abiotique occupé par les espèces au sein d'une région.

Chapitre I

Plants show different types of responses to the environment at different scales: trait means and phenotypic integration

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Soumis à *Plant Ecology*

Plants show different types of responses to the environment at different scales: trait means and phenotypic integration

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I. Abstract

Understanding plant phenotypic responses to abiotic variation is central to ecology. In this response, not only shifts in mean phenotypes may be important, but also in phenotypic integration, i.e. number and strength of correlations between phenotypic traits. However the relative importance of different phenotypic responses has seldom been studied in the field. Also, responses may vary with spatial scale. This study examined the variation in mean traits (growth, reproduction and reproductive strategies), and in phenotypic integration, between low and high altitudinal populations of the Kerguelen Cabbage (*Pringlea antiscorbutica*, Brassicaceae) at both small and large spatial scales. We found distinct changes in mean traits and in phenotypic integration with altitude likely reflecting strong abiotic constraints at high altitudes and increased competition at low altitudes. Overall, changes in phenotypic integration with altitude were as strong as changes in trait means, but did not occur at the same spatial scale: phenotypic integration showed higher variation at small spatial scales and much lower variation at large spatial scales. The increase in phenotypic integration with altitude at small spatial scales may explain why changes in reproductive strategies at large scales were not sufficient to compensate the effect of altitude on plants. This could be explained by the increasing stress at high altitudes limiting response strategies to parallel shifts of all intercorrelated traits. These results highlight that plants can exhibit in the field different phenotypic responses at different spatial scales and that changes in phenotypic integration at small scales may limit changes in reproductive strategies at large scales.

Key-words: altitudinal variation, growth and reproductive traits, *Pringlea antiscorbutica*, sub-Antarctic Kerguelen and Crozet Islands, trait correlations.

II. Introduction

The study of how plant phenotypes respond to environmental variations is one of the corner-stones of ecology (Schimper 1903) and is essential for understanding and predicting how plants respond to environmental change. Phenotypic response to environmental variation has classically been studied by looking at changes in the mean values of traits (Totland & Birks 1996; Cronin & Lodge 2003; Murray et al. 2003). However, the phenotype expressed by plants in a given environment may represent the pattern of functional, developmental and/or genetic correlations among their traits (Pigliucci 2003). Greenhouse experiments indicate that the intensity of such phenotypic integration (i.e. number of significant correlations among traits) may change with environmental conditions (Schlichting 1989a, b; Gianoli 2004; Waitt & Levin 1993; Sleeman et al. 2002; Pigliucci & Kolodynska 2006). But greenhouse experiments are inherently restrictive because studies can not completely mimic the combinations of abiotic and biotic factors that plants are facing in the field. Therefore, the resulting phenotypes are not the outcome of plant development as it occurs in the field. To the best of our knowledge, changes in phenotypic integration have so far not been explored in the field.

How mean traits and correlations between traits change in response to the environment may reveal different types of phenotypic responses in plants. On the one hand, a shift in means likely reflects a change in the vitality or in the growth and reproductive strategies of an average individual from a local population due to a shift in resource levels or climatic constraints (Grime 2001; Cronin & Lodge 2003; Willis and Hulme 2004). On the other hand, increases in correlations between traits might reflect increasing internal genetic, functional, developmental and/or energetic constraints, permitting only certain trait combinations to be realized across all individuals of a local population (Schlichting 1989a; Waitt & Levin 1998; Gianoli & Palacio-Lopez 2009). Despite potential interest in understanding the response of phenotypes to

environmental variation, the relative importance of changes in trait correlations as compared to changes in mean values is yet to be studied.

Numerous studies have shown responses of plant phenotypes across large spatial scales (i.e. changes in species traits along multi-regional or worldwide environmental gradients, Moles & Westoby 2003; Midgley et al. 2004, Moles et al. 2005) or across small spatial scales (i.e. changes in traits along regional gradients, Totland & Birks 1996; Díaz et al. 1998; Luizão et al. 2004; Jung et al. 2008). However, to the best of our knowledge no study has aimed at investigating the responses of plant phenotypes to environmental variation across different scales. It hence remains unknown whether plants differently respond to environmental change at large and at small spatial scales.

For studying shifts of both trait means and phenotypic integration along both small and large scale environmental gradients, we need (i) a strong abiotic spatial gradient, (ii) plant species that occupy the majority of this gradient, (iii) plant communities that have been minimally disturbed by human activities, allowing the study of species along their entire abiotic spatial distribution. All three of these criteria are met on the sub-Antarctic Kerguelen and Crozet islands (Smith 1984; Frenot et al. 2001; Hennion et al. 2006b) for one of the dominant species on these islands, the Kerguelen Cabbage (*Pringlea antiscorbutica* R. Br.) (Hennion & Martin-Tanguy 2000). Strong phenotypic variation has been described as occurring in this species, in particular traits related to reproduction or size have been reported to vary (Werth 1911; Chapuis et al. 2000, Schermann-Legionnet et al. 2007). Such life history traits are particularly likely to respond to environmental changes (Cornelissen et al. 2003; Larcher 2003).

We studied *P. antiscorbutica* sampled from different altitudes in Iles Kerguelen and Iles Crozet. We considered population means of life history traits in order to characterize the sheer sizes of individuals. We studied population means of ratios between the organs of plants in order to characterize the strategy of relative investment in particular life history functions (e.g.

the ratio between total mass of seeds produced by the plant and plant volume indicates investment into reproduction vs. vegetative growth). We also studied within-population correlations between traits to characterize phenotypic integration between traits. We considered both trait correlations reflecting life history trade-offs and those reflecting life history allometries. We compared these measurements between lower and higher altitudinal populations. We performed the comparisons at small spatial scales (populations separated by distances of less than 6700m, see Methods) and at larger spatial scales (populations separated by distances of more than 6700m), in order to investigate the responses of the *P. antiscorbutica* phenotype to altitude across the two spatial scales separately. We asked: Does the Kerguelen Cabbage phenotype respond to environmental changes with altitude by a change in mean phenotype or rather through a change in phenotypic integration? We went on to ask if changes in phenotypic integration are relatively more important at small or at large spatial scales?

III. Materials and Methods

III.1. Material

III.1.1. Study area

The circumpolar sub-Antarctic region extends between latitudes 46° and 55° S, including Iles Crozet and Iles Kerguelen in the Southern Indian Ocean (Hennion & Martin-Tanguy 2000) (Fig. I.1a). These islands host strong spatial abiotic gradients, in particular they have one of the steepest altitudinal temperature gradients in the world, on average temperature decreases by 0.8°C per 100m in Iles Kerguelen (Hennion et al. 2006b). The islands contain species-poor plant communities that are relatively undisturbed by human activities (Smith 1984; Frenot et al. 2001), this allows species to be studied across their entire abiotic range.

III.1.2. Study species

Pringlea antiscorbutica is a large and prominent rosette plant (Fig. I.1d, e) that is endemic to a few sub-Antarctic islands within the southern Indian Ocean (Marion Island, Prince Edward Island, Iles Crozet, Iles Kerguelen, Heard Island and McDonald Island) (Hennion & Walton 1997a). This crucifer covers a wide range of habitats from the shore up to approximately 1,000 m above sea level, for the most part it is found in meadows, herbfields, mires, flushes, fellfields on mountains, and along streams or drainage lines. *P. antiscorbutica* preferentially colonizes well-watered and well-drained areas (Hennion & Walton 1997a). *P. antiscorbutica* is a perennial plant with exclusively sexual reproduction, the mature individuals produce annually a particularly large number of seeds for a subantarctic species (Hennion & Walton 1997b; Schermann-Legionnet et al. 2007). *P. antiscorbutica* is self-compatible and wind and/or autonomous pollinated (Schermann-Legionnet et al. 2007). Seed dispersal between islands through club floating in seawater has been observed in Kerguelen (Chapuis et al. 2004), but freshwater or wind dispersal does not exceed a few meters (Schermann-Legionnet et al. 2007).

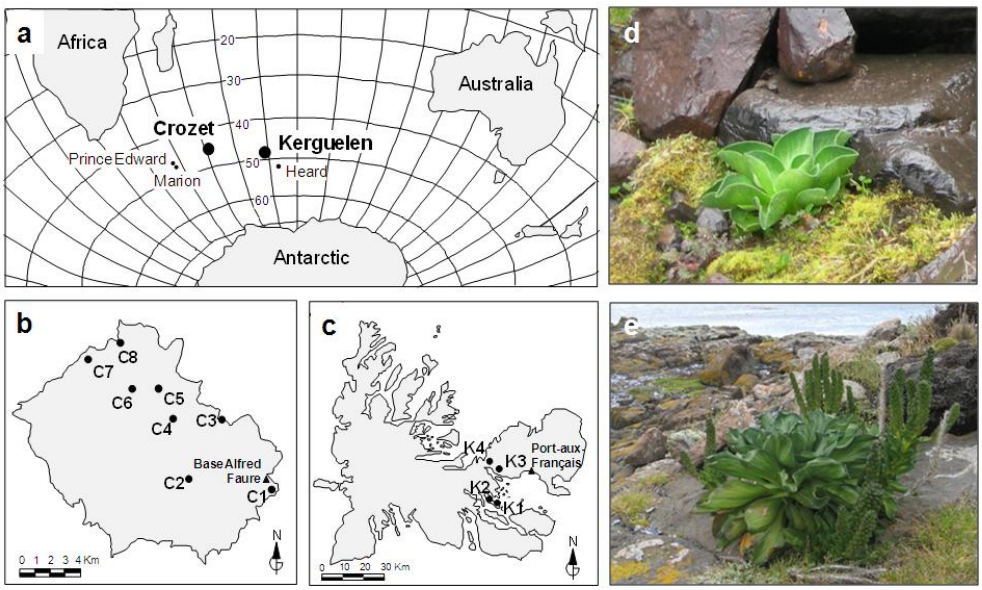

Figure I.1 (a) Geographical position of Iles Kerguelen and Iles Crozet in the South Indian Ocean. Localities of the sampling sites (b) in Iles Crozet and (c) in Iles Kerguelen. Pictures of typical phenotypes of *Pringlea antiscorbutica* d) at high altitudes and e) at low altitudes.

III.2. Sampling

We studied twelve populations of *P. antiscorbutica* at eight sites in Crozet (C1 to C8) in 2003 and at four sites in Kerguelen (K1 to K4) in 2004 (Table I.1; Fig. I.1b, c). The sites were chosen to cover the altitudinal range of the species in Crozet and Kerguelen, from 20m to 600m a.s.l.

We sampled 15 to 20 individuals per site during the summer campaigns (December – February). Sampling was focused on plants that had reached the same phenological stage, i.e. just before fruit dehiscence when seeds are mature. During the period of study, fruit dehiscence occurred from January onwards in the earliest flowering stands but not before March in the mountain stands. We limited how much bias in plant size variation could be due to variation in plant age by sampling only reproducing individuals (plant size has been shown to change only little after reproductive maturity; Chapuis et al. 2000). We sampled 15 fruits from the highest inflorescence of each plant sampled and 15 more fruits from another randomly selected inflorescence. Fruits were stored at 4°C. Subsequently, seeds were dried at 80°C until no more weight loss from moisture could be measured.

Table I.1 Description of the sites on Ile de la Possession (Iles Crozet) and on Iles Kerguelen during the summers of 2003 and 2004 respectively: localities, altitude (m) and numbers of plants sampled for each particular collection (see Fig. I.1 for site localities).

Island	Site	Locality	Altitude (m)	Number of sampled plants
Ile de la Possession (Iles Crozet)	C1	Base Alfred Faure	50	20
	C2	Rivière du Camp	320	20
	C3	Baie Américaine	20	15
	C4	Mont de l'Alouette	60	15
	C5	Monts Jules Verne	360	15
	C6	Monts Jules Verne	440	20
	C7	Grande Coulée	200	15
	C8	Cap Vertical	100	15
Iles Kerguelen	K1	Australia	8	20
	K2	Australia	100	20
	K3	Val Studer	371	20
	K4	Val Studer	600	20

III.3. Trait measurements

III.3.1. Raw measurements

We measured plant diameter and plant height and from this estimated plant volume as a cylindrical volume. We counted the total number of inflorescences and we measured the height of the fertile part of each inflorescence. This data was used to estimate the total number of fruits on each plant, estimations were made using an adapted extrapolation formula of Schermann-Legionnet et al. 2007:

(1) $$n_{ftot} = \left[53.03 + \left(4.03 * \overline{h_i}\right)\right] * n_i$$

with $\overline{h_i}$ the mean height of the fertile part of inflorescences and n_i the number of inflorescences on the plant.

For each of the 15 fruits sampled per plant, we counted the number of seeds and we weighed the total mass of seeds with a precision balance (±0.01g precision). We also measured the length of seeds with a binocular loupe equipped with a micrometer to the nearest 5 µm. Mass and length measurements were $\log_{10}$-transformed to approach homogeneity of variance for the residuals; this was requisite for later analyses. For each plant we calculated mean seed number per fruit, individual log seed mass and individual seed length across the 15 sampled fruits. Total number of seeds produced by a plant was calculated as the product of the average number of seeds per fruit and total number of fruits on the plant (see above). Total mass of seeds produced by a plant was estimated as the product of mean individual seed mass and the total number of seeds produced by the plant, total mass of seed per plant was subsequently $\log_{10}$-transformed.

III.3.2. Ratios

For each plant we calculated the ratio [plant height / plant diameter] as an indicative measure of the relative growth invested into competition for light (vertical growth) versus the investment

into minimising wind damage (horizontal growth). Similarly, we calculated for each plant the ratio [log individual seed mass / total number of seeds] to estimate the relative investment into quality versus quantity of seeds. The ratio [log individual seed mass / number of seeds per fruit] provided the same estimated measure of investment into quality versus quantity of seeds, but is independent of plant size. Finally, for each plant we calculated the ratio [log total mass of seeds produced by the plant / plant volume] to evaluate the relative investment in growth versus reproduction. We excluded three outliers from the ratio [individual seed mass / number of seeds per fruit], the ratio [individual seed mass / number of seeds per plant] and the ratio [total mass of seeds per plant / plant volume] in order to approach homogeneity of variance for the residuals in later analyses.

III.3.3. Trait correlations

We selected trait correlations that reflect the strength of either allometries, broadly defined as positive relationships between traits in individuals, or trade-offs, here defined as negative relationships between traits in individuals. Using Pearson correlation, we correlated, in each site, plant height against plant diameter, plant volume against total number of seeds produced by the plant, individual seed mass against the number of seeds per fruit, and individual seed mass against total mass of seeds produced by the plant. The existence of such correlations in plants is well documented (Convey 1996; reviewed in Grime 2001). For all traits included in these within-site correlations, variance within-site was important, accounting for 14% to 71% (mean 43%) of the total variance across sites and isles. We did not z-transform the correlation coefficients, as the sets of correlation coefficients were normally distributed.

III.4. Statistical analysis

We calculated the geographical distance between the sites from their GPS coordinates using the geographical information system software ArcView. We only estimated the within-island distances (i.e. between sites within Crozet and between sites within Kerguelen), because the between-island distances are by orders of magnitude larger than the within-island distances. We estimated the physical distance between the sites from the straight distance given by ArcView and the altitudinal difference between the sites, using Pythagoras theorem. The distance between sites ranged from 796m to 23,711m. The median of the set of distances was 6700m. We hence conducted 17 pairwise comparisons between low-altitudinal and high-altitudinal sites separated by distances of 6700m or less, and 17 pairwise comparisons between sites separated by larger distances.

Changes in the means of absolute trait values and ratios, and in correlation coefficients in response to altitudinal variations (between the higher and lower sites within altitudinal comparisons) were analysed by a pairwise Student's t-test (Statsoft 2010). The analysis was performed across the set of altitudinal comparisons at large spatial scales and across the set of altitudinal comparisons at small spatial scales. Because we compared sites two by two, a given site was included several times within the same set of altitudinal comparisons. To deal this statistically, we adjusted the degrees of freedom to the actual number of sites included in the analysis (minus 1). In order to ensure that a difference in phenotypic response between the two spatial scales does not simply reflect a difference in the altitudinal ranges, we verified that the altitude ranges covered by the individual small-scale comparisons were not different than those covered by the individual large-scale comparisons (ANOVA: $F(1,32) = 1.22$; p (adjusted) = 0.38).

We tested whether altitudinal changes in trait means and trait correlations differed between small and large spatial scales by comparing the effect sizes of altitude between both scales. For

each trait mean and correlation, we calculated the effect size as a Fisher coefficient Zr from the t-value of the pairwise Student test (Rosenthal 1984). We used the actual number of sites included in the comparisons to calculate the Zr coefficient. We calculated the difference between the Zr from the large spatial scales comparison and the Zr from small spatial scales comparison (Snedecor and Cochran 1967 cited in Rosenthal 1984). As above, we used the actual number of sites included in the comparisons to calculate the Zr of the difference. We test the significance of the Zr of the difference with a two-tailed p-value associated to that Zr using a statistical table ($n = 12$; $\alpha = 5\%$).

IV. Results

IV.1. Changes in mean traits: mainly at large spatial scales

At large spatial scales, we found significant changes in the means of seven of the twelve traits studied (Fig. I.2). Plant height, individual seed length, individual seed mass, mass of seeds per fruit, total mass of seeds produced by a plant, the ratio [plant height / plant diameter] and the ratio [individual seed mass / number of seeds per fruit] were significantly smaller at the higher altitudes. Five trait means showed no significant changes, this included the ratio [total mass of seeds produced by the plant / plant volume] which characterizes the relative reproductive investment of the plants. Plant diameter and the number of seeds per fruit did not change, indicating that declines in the ratios [plant height / plant diameter] and [individual seed mass / number of seeds per fruit] with altitude were essentially due to declines in plant height (flatter plants, but not more horizontal growth) and in individual seed mass (smaller but not more numerous seeds) respectively. At small spatial scales, we found changes in the means of only two of the twelve traits studied (Fig. I.2): individual seed mass and the ratio [plant height / plant diameter] were smaller at the higher altitudes.

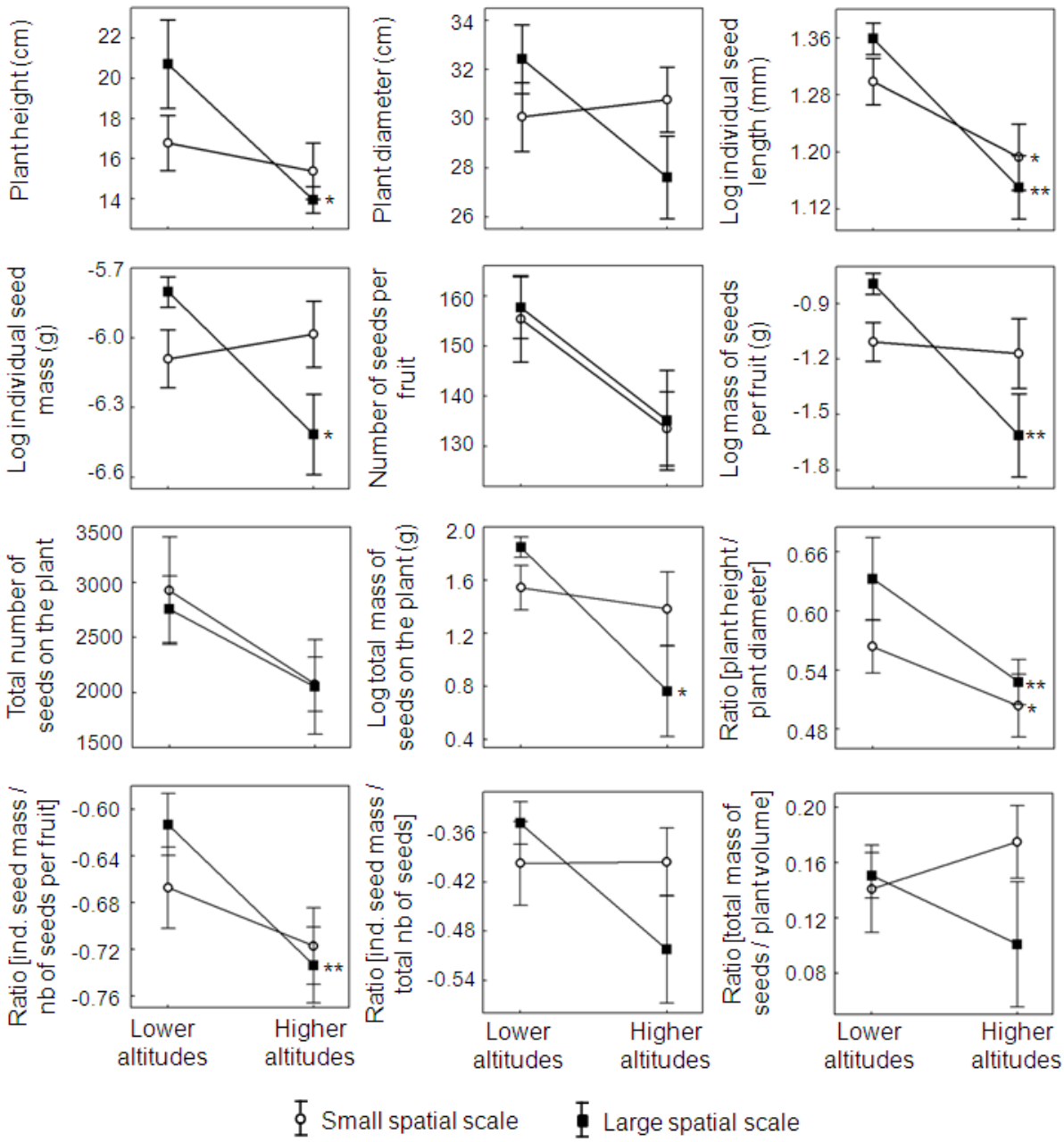

Figure I.2 Means of life-history traits compared between high and low altitudinal sites and analysed at small spatial scales (open circles) and at large spatial scales (dark squares). Means (± SE) are given. Asterisk indicate a significant difference in trait means between higher and lower altitudes (* $p < 0.05$; ** $p < 0.01$)

IV.2. Changes in trait correlations: mainly at small spatial scales

At large spatial scales, only one trait correlation changed (Fig. I.3): the correlation between plant height and plant diameter was stronger at the higher altitudes. At small spatial scales, the all four studied correlations changed (Fig. I.3). We found significant increase in the positive correlation between plant height and plant diameter, in the positive correlations between plant volume and total mass of seeds produced by the plant and in the negative correlation between individual seed mass and number of seeds per fruit at the higher altitudes. In contrast, the correlation between individual seed mass and the total number of seeds produced by the plant was found to be weaker at the higher altitudes.

IV.3. Comparison between small and large spatial scale: few significant differences between effect sizes

The absolute effect sizes from altitudinal comparisons were higher at large spatial scales than at small spatial scales for ten of the twelve trait means studied (Fig. I.4). Inversely, the absolutes effect sizes of correlations were lower at large spatial scales than at small spatial scales for the four correlations studied. However, these differences between large and small spatial scales were significant (two-tailed p-value < 0.05) for only one trait mean, that being individual seed mass.

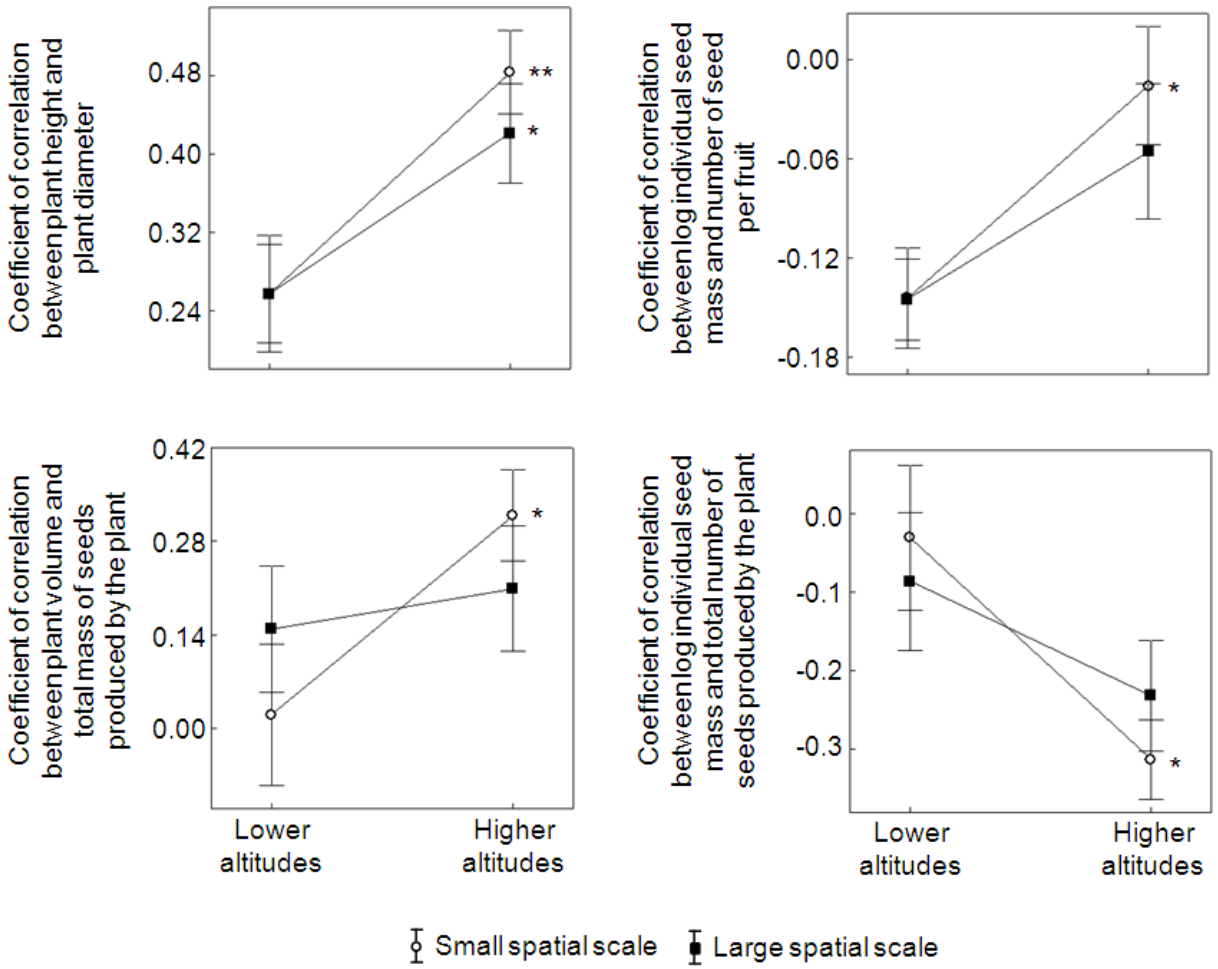

Figure I.3 Correlation coefficients between life-history traits compared between high and low altitude sites and analysed at small spatial scales (open circles) and at large spatial scales (dark squares). Means (± SE) are given. Asterisk indicate a significant difference in correlation coefficients between higher and lower altitudes (* $p < 0.05$; ** $p < 0.01$)

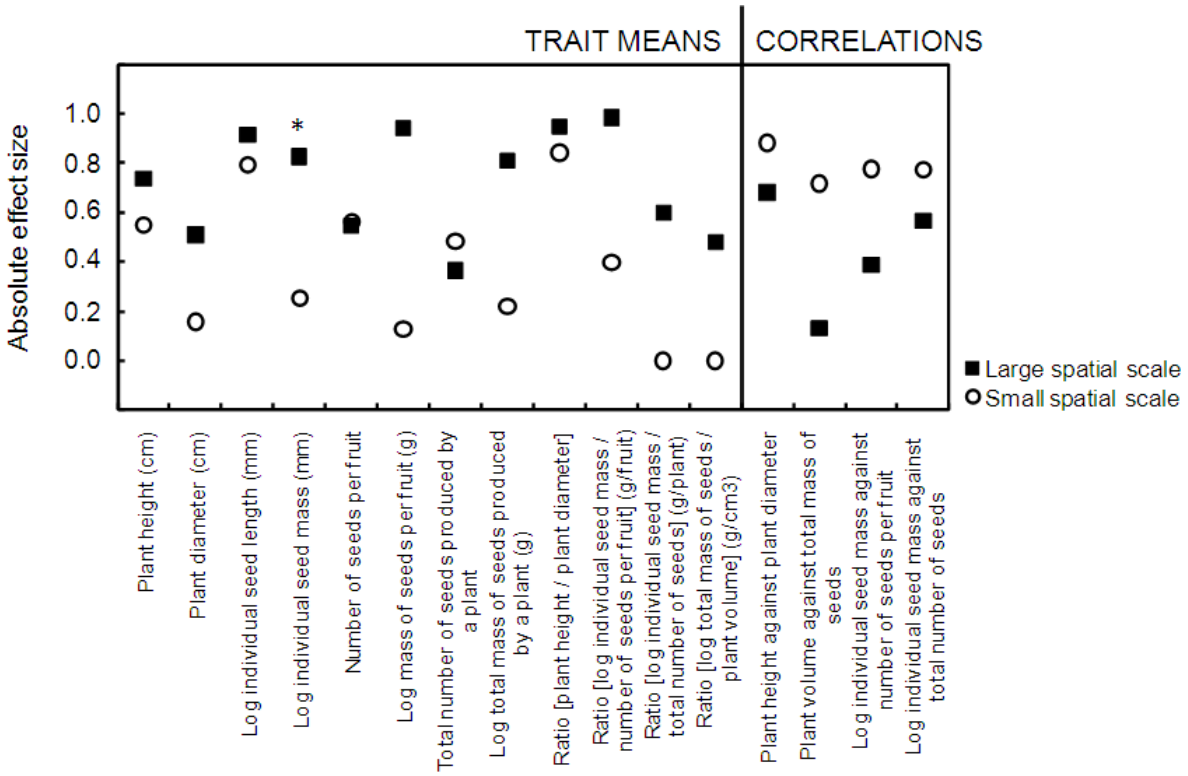

Figure I.4 Absolute effect sizes of differences of traits between high and low altitude sites at small spatial scales (open circles) and analysed at large spatial scales (dark squares). Traits are measured as mean values and as correlations among traits (left and right part, respectively, of the graph). Asterisk indicate a significant difference in effect sizes between small and large spatial scales (* $p < 0.05$)

V. Discussion

This study was the first to explore the importance of changes in phenotypic integration in the field. Changes in phenotypic integration with altitude were equally as important as changes in trait means. However, changes in phenotypic integration did not occur at the same spatial scale as changes in trait means. Even though changes in trait means and in phenotypic integration within altitudinal comparisons did not significantly differ between scales, phenotypic integration did exhibit higher variation at small spatial scales and a much lower variation at large spatial scales. These results highlight that plants can exhibit different phenotypic responses at different spatial scales, and that we need to consider changes in phenotypic integration to depict responses at small scales.

V.1. Phenotypic responses of *P. antiscorbutica* to altitude

V.1.1. Response to abiotic conditions at high altitudes

Plant size, individual seed length, individual seed mass and total mass of seeds produced by a plant decreased on average with altitude. Decreases in vegetative size and reproductive capacity with altitude are classical responses of plants linked to increasing abiotic stress (Smirnoff 1995; Körner 1999). Moreover, changes in phenotypic integration indicated trait co-adjustments within *P. antiscorbutica* populations at the higher altitudes. The negative correlations between mean seed mass and seed quantity suggests a trade-off between these traits. The positive correlations between plant diameter and plant height and between plant volume and total mass of seeds produced by the plant imply allometric relationships between these traits. The increase in most of these correlations at the higher altitudes suggests a limitation to how plants can adjust their traits in response to increasing abiotic stress. We show that the increase in phenotypic integration under abiotic stress that has been observed in simplified environments in greenhouse experiments (Schlichting 1989a, b; Waitt & Levin

1993; Sleeman et al. 2002; Gianoli 2004; Pigliucci & Kolodynska 2006) is also encountered in natural environments, under complex combinations of abiotic and biotic constraints. In Kerguelen, high altitude environments are characterized by several limiting abiotic factors, i.e. nutrient-poor stony soils, low temperature, strong winds, frequent freeze-thaw alternations and mechanical stress. These extreme abiotic conditions might not only induce reduced growth and reproductive capacity but also constrain plants in their variability of forms and reproductive strategies.

V.1.2. Inverse changes in the relative importance of competition and abiotic stress with altitude

We found a decrease in the ratio [plant height / plant diameter] with increasing altitude, essentially an adjustment to a flatter form. While diameter remains constant, plants at low altitudes are taller, whereas plants at higher altitudes are very flat to the ground. Plant form at low altitude likely reflects local competition and relatively little abiotic stress whereas a prostrate stature at higher altitudes is likely to reflect a response to strong abiotic stresses (Körner 1999). Indeed, at low altitudes, *P. antiscorbutica* is found in moist and relatively fertile sheltered habitats as dense populations within a closed herbfield of forbs (Hennion et al. 2006b). At higher altitudes this vegetation quickly gives way to fellfield, with its associated harsh abiotic conditions as described above. Fellfield is characterized by scattered vegetation dominated by cushion-forming forbs, short grasses, mosses and lichens (Smith 1984; Hennion et al. 2006b). Inverse changes in biotic (i.e. competition) and abiotic constraints are therefore likely with increasing altitude and result in changes of plant form. Moreover, we found a decrease in the ratio [individual seed mass / number of seeds per fruit]. Plants invested less at higher altitude, producing smaller seeds while number of seeds remains constant. This shift in reproductive strategy, which favors seed quantity to the detriment of seed quality may result

from decreasing competition pressure, i.e. the decreasing need to produce the highly competitive offspring that result from large seeds (Tungate et al. 2002, 2006).

V.2. Phenotypic responses to altitude depend on the spatial scale

The relative importance of changes in trait means and in phenotypic integration varied between scales. The mean phenotypic responses at large spatial scales might reflect long-term evolutionary responses to environments more or less at the biological limit of the study species. The changes in phenotypic integration at small spatial scales may constitute fine scale and reversible adjustments to small environmental variations. Given the relatively low dispersal capacity in *Pringlea* across large distances (Hennion & Walton 1997a; Schermann-Legionnet et al. 2007), the difference in phenotypic responses between sites separated by increasingly large geographical distances may be partially linked with a decline in gene flow with increasing distance between populations. This hypothesis should be addressed in future research.

The large-scale changes in trait means may result from changes in phenotypic integration at small scales. At large scales, changes in the ratios [plant height / plant diameter] and [individual seed mass / number of seeds per fruit] may be not sufficient to compensate the effect of altitude on plants. The decline in plant height with increasing altitude was not compensated for by larger plant diameter and the decline in individual seed mass was not compensated for with more numerous seeds, both growth and reproduction decreased with altitude. Moreover, it is particularly impressive that our measure of reproductive investment (ratios of total seed mass and plant volume) did not change with the environment at any scale. This goes counter to classical patterns of trait variation of plants under stress (e.g. Grime 2001). A possible explanation for this result might be the strong increase in phenotypic integration with stress. In fact, phenotypic integration has been shown to correlate with reduced phenotypic plasticity (Gianoli & Palacio-Lopez 2009). Plasticity in itself may be a condition for a shift in

reproductive investment, a plant might restrict its growth in order to have more resources available later for reproduction. This and numerous other examples of plastic shifts in reproductive investment might start with an independent shift of one trait, forcing the ensuing responses of other traits. If from the onset any shift in one trait is blocked by phenotypic integration with other traits, no shifts in reproductive investment are to be expected. Response to increasing stress at high altitudes would then be limited to a decrease in the size of the entire plant with all its intercorrelated traits, which is what we observed.

VI. Conclusion

This study was the first to explore the importance of changes in phenotypic integration in the field. We show that changes in phenotypic integration with altitude were as strong as changes in trait means, but did not occur at the same spatial scale: phenotypic integration showed higher variation at small spatial scale and a much lower variation at large spatial scale. We suggest that changes in mean traits and phenotypic integration with altitude reflect strong abiotic constraints of high altitude environments and the increased competition of low altitude environments. Changes in reproductive strategies at large scales were not sufficient to compensate the effect of altitude on plants. This may be explained by the increase in phenotypic integration at small spatial scales, a response to increasing stress at high altitudes would be limited to parallel declines of all intercorrelated traits. These results highlight that plants can exhibit different phenotypic responses at different spatial scales and that responses at small scales may impact on responses at large scale. Our results advance the understanding of the subtle mechanisms of phenotypic response of plants to their environment, therefore improving our capacity for predicting plant response to climate change.

VII. Acknowledgements

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Chapitre II

Endemic species have highly integrated phenotypes, environmental distributions and phenotype/environment relationships

Hermant Marie, Prinzing Andreas and Hennion Françoise

En préparation

Endemic species have highly integrated phenotypes, environmental distributions and phenotype/environment relationships

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I. Abstract

Why are endemic species geographically restricted? Ecological explanations suggest that endemics are specialized either on narrow or on particularly stressful habitats, both linked to narrow phenotypic variability. However, variability *per se* may not suffice to reflect the interactions within and between complex phenotypes and complex environments. Here, we suggest that endemics are phenotypically and environmentally more integrated, with strong intercorrelations both among different phenotypic traits, among conditions occupied along different environmental gradients, and among traits and environments occupied. We measured distribution, flowering phenology and multiple aspects of plant size along three types of abiotic environmental gradients in fourteen plant species present in the Kerguelen Islands and ranging from highly endemic to cosmopolitan. We found that mean trait values and variabilities of species were independent of their level of endemism. The position of a species along environmental gradients depended on its level of endemism: endemics occupied higher and less variable positions along the altitudinal gradient and lower positions along the salinity gradient. Phenotypic integration among traits (here estimated through the percentage of variance captured by the first axis of a PCA across all traits) increased with the endemism level of species. Similarly, environmental integration of distributions along the three gradients increased with the endemism level of species. Finally, the correlations between traits and each of the three environmental gradients increased with the level of endemism. These results suggest that the higher its integration within and between phenotypes and environments, the more restricted the area of a species is. These phenotypic characteristics of endemic species may result in their lower capacity to respond to novel environmental conditions.

Key-words: abiotic environmental gradients, biogeography, climate change, correlations traits / environments, endemism level, environmental positions, life-history traits, multi-species

comparison, phenotypic integration, environmental integration, sub-Antarctic Kerguelen Islands

II. Introduction

Endemic species are, by definition, geographically restricted (Kruckeberg & Rabinowitz 1985). The causes of such limited distribution ranges have been discussed since the early times of biology (de Candolle 1855) and remain unknown nowadays. It has been argued that endemism may result from the increasing restriction of the species habitat over time (paleoendemism, Stebbins & Major 1965). In this context, the cause of endemic distribution may be specialization to particular ecological conditions (Stebbins 1980), where species may maximize performance (survival and reproduction), but may be unable to occupy other environments (Meyer 1986; Caley & Munday 2003). However, the hypothesis of such trade-off between performance and distribution range was not systematically supported by comparative studies of endemic and widespread species (Matesanz et al. 2009). Another explanation is that endemic species are not specialist to their habitat, but may find refuge in stressful habitats where inter-specific competition is reduced (Gankin & Major 1964; Lavergne et al. 2003, 2004). They may exhibit particular traits associated with stress tolerance, low competitiveness or low dispersal ability (Drury 1974; Lavergne et al. 2003, 2004). However, such biological attributes may not always suffice to highlight specific properties of endemics or to differentiate them from their widespread congeners (Fiedler 1987; Matesanz et al. 2009). Finally, some authors proposed that endemic species may be restricted to particular environments because they are less variable in phenotype than more widespread species (Rapson & Maze 1994; Sultan 2001). But, phenotypic variability alone may not reflect the complex nature of species phenotypic response to environmental variations (Richards et al. 2005). In this study, we introduce phenotypic and environmental integration as a new factor contributing to endemism. We hypothesize that

species with higher endemism level may be more integrated than more widespread species, with stronger intercorrelations among different phenotypic traits, among conditions occupied along different environmental gradients, and among traits and environments occupied.

First, a strong phenotypic integration (i.e. strength of correlations among traits) within a species may result in a restriction of its distribution range. Indeed, increases in correlations between traits likely result in permitting only certain trait combinations to be realized across all individuals of a species, due to increasing internal genetic, functional, developmental and/or energetic constraints (Schlichting 1989a). A strong phenotypic integration within a species may reflect a lower multivariate phenotypic variability, since the greater a given phenotypic trait is linked with other traits, the more limited its range of variation is (Gianoli & Palacio-Lopez 2009) (Fig. II.1a). But, it may also reflect a limitation in how a species can adjust its traits to environmental variations, as correlated traits respond similarly to a change in the environment (Schlichting 1989b) (Fig. II.1b).

Second, a strong environmental integration, i.e. strength of correlations among abiotic conditions where species occur, within a species may imply a restriction of its ecological distribution (Levins 1968). Like with phenotypic integration, we consider that strong environmental integration may result in a restriction of all individuals of a species to occur in only certain combinations of abiotic conditions. It may also indicate low variability in environmental conditions occupied by a species. A strong environmental integration may thus constrain species to occupy particular habitats and may lead to endemism if these habitats are geographically restricted.

Finally, strong correlations between traits and abiotic variables in a species may induce reduction of geographical distribution. In a given region, such correlations imply that the amount of trait variability released by a species at any one time is fully invested in a close adjustment to the environment occupied by the species. Ultimately, this may result in a

specialization of species to particular habitats and may lead, once again, to endemism if these habitats are geographically restricted.

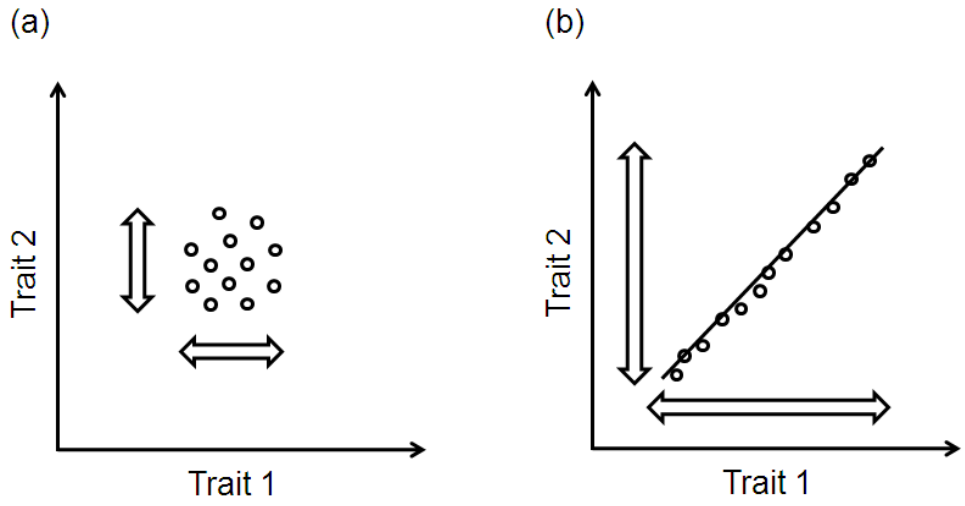

Figure II.1 Schema of the two extreme alternative explanations for a strong phenotypic integration (i.e. strength of correlations among traits). (a) A strong phenotypic integration within a species may reflect low multivariate trait variability (represented here by the white arrows) or (b) may reflect a limitation of species to realize only certain combinations of traits (represented here by the linear adjustment). In this case, trait variability may be high. One point is one individual of the studied population of plants. Intermediate states are possible. The same explanations can be applied to environmental integration.

To account for phylogenetic effects, ecological and biological traits are often compared between congeneric endemic and widespread plant species (Baskauf & Eickmeier 1994; Brown et al. 2003; Matesanz et al. 2009). However, the observed patterns could be specific to lineages and some authors have pointed out that samples of species from various lineages must be studied to provide generalizations (Bevill & Louda, 1999; Gitzendanner & Soltis, 2000; Lavergne et al. 2004). Moreover, such comparisons are often performed between plant species in two extreme cases of distribution ranges (i.e. narrow endemic *versus* widespread distributions; Baskauf & Eickmeier 1994; Lavergne et al. 2003, 2004; Matesanz et al. 2009). However, a more powerful approach to study the links between geographical distributions and trait or environmental variation could be to compare species with gradually increasing distribution ranges.

As differences in regional histories can strongly affect observed patterns of endemism (Cowling et al. 1994), comparative studies should be made in a single regional flora (Lavergne 2003, 2004). Oceanic islands are recognized to be especially rich in endemic species (Kruckeberg & Rabinowitz 1985). The sub-Antarctic Kerguelen Islands are of particular interest for our study because they host a large panel of plant species which vary in their geographical distribution ranges and which co-exist along strong abiotic gradients (Hennion & Walton 1997a; Frenot et al. 2001; Hennion et al. 2006a). Moreover, the species are distributed within each of three major lineages: Poales, Ranunculales, and Core Eudicots. We hypothesize that endemic species are phenotypically and environmentally more integrated than species with wider distributions. More precisely, we hypothesize that an increasing endemism level of plant species is related to (i) increasing phenotypic integration, (ii) increasing environmental integration and (iii) strengthening of correlations between traits and abiotic environments. We measured these environmental and phenotypic characteristics within standard gradients of salinity, moisture and altitude in fourteen plant species growing in Kerguelen Islands. We also tested for the relationships between endemism and either phenotypic variability, mean trait values, environmental variation and environmental position. We accounted for species phylogenetic positions, autochthonous or introduced origins and life-history traits in the observed patterns.

III. Material and Methods

III.1. Study sites

The sub-Antarctic region extends between latitudes 46° and 55° S, including the Kerguelen Islands in the Southern Indian Ocean (Hennion & Martin-Tanguy 2000) (Fig. II.2a). We worked at four sites in the eastern part of the Kerguelen Islands (Fig. II.2b). The three coastal

sites (Ile Australia, Ile Guillou and Isthme-Bas) were chosen for their strong salinity and moisture gradients. The inland site (Val Studer) was chosen for its steep altitudinal temperature gradient (Hennion et al. 2006a). In each site, we established from three to nine transects of three sampling points, between which we maximized differences in salinity, moisture or altitude. We multiplied each type of transects (salinity, moisture or altitude) in order to cover the differences in other abiotic factors (e.g. wind exposure, edaphic conditions) and thus minimize their effect. One of the altitudinal transects was formed of only two sampling points, as the intermediate altitudinal section of this transect was inaccessible. In summary, we established a total of 22 transects and 65 sampling points over the four sites.

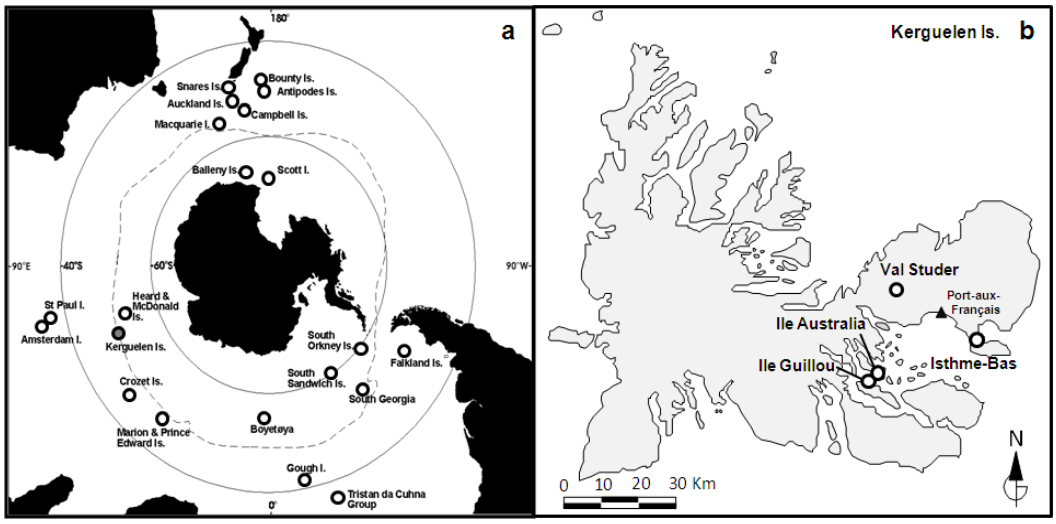

Figure II.2 (a) Map of lands and islands in the southern hemisphere and (b) location of our four sampling sites in Kerguelen Islands.

III.2. Study species

We selected fourteen plant species according to two prerequisites (Fig. II.3). First, we worked on plant species which gradually vary in their geographical distribution ranges. We obtained the geographical distribution information for species from Lourteig & Cour (1963), Walton (1979), Frenot et al. (2001) and Van der Putten et al. (2010). We assigned different levels of

endemism to the studied species according to their geographical distribution (Fig. II.2a and II.3): (1) endemic to the south Indian ocean province, i.e. distribution restricted to one or a few islands among Kerguelen Is., Crozet Is., Marion and Prince Edward Is., and Heard and McDonald Is.; (2) endemic to the same province plus Macquarie I.; (3) austral circumpolar, i.e. distribution restricted to the circumpolar region; (4) austral, i.e. distribution including the circumpolar region and southern lands (South America, New Zealand…); (5) widespread, i.e. worldwide distribution.

The second prerequisite concerned ecological and demographic characteristics of species described as follows: (i) each studied species has at least one large population in the study area; (ii) each species has a large distribution along the studied abiotic gradients, i.e. is present in sufficiently contrasted conditions of altitude, moisture and salinity; (iii) species co-exist within our sampling points. As no species have exactly the same ecological requirements in the study area, the last criterion could not be completely filled: the number of species sampled per point ranged from one to fourteen.

We compiled information on phylogenetic relationships, origins and life-histories of the fourteen studied species from field observations and literature (Fig. II.3). The species nomenclature followed Van der Putten et al. (2010). The species taxonomic positions were obtained from the Angiosperm Phylogeny Group III (Bremer et al. 2009). The autochthonous or introduced origins of species to Kerguelen Islands were established from Frenot et al. (2001). Growth forms, dispersal modes and types of reproduction were determined in the field and from literature (Chastain 1958; Cour 1958; Tallowin & Smith 1977; Convey 1996; Hennion & Walton 1997b; Durka 2002; Pakeman et al. 2002; Robinson et al. 2003; Chapuis et al. 2004 and Schermann et al. 2007; Kleyer et al. 2008).

Figure II.3 Phylogenetic relationships, geographical distributions and the corresponding endemism levels (see Methods), origins, types of reproduction, seed dispersal modes, vegetative dispersal modes and growth forms of the fourteen studied species in Kerguelen Islands. The species nomenclature followed Van der Putten et al. (2010). The species taxonomic position was obtained from the Angiosperm Phylogeny Group III (Bremer et al. 2009). Origins are Auto: autochthonous; Intr: Introduced to Kerguelen Is. after the start of human visits in 1772. Types of reproduction are S: by seed; SV: by seed and vegetatively. Dispersal modes are Ane: anemochorous; Hyd: hydrochorous; Zoo: zoochorous and Clo: Clonal. Growth forms are Cu: cushion; Br: branched; Ro: rosette; Tu: tuft.

Family	Genus / Species	Geographical distribution	Endemism level	Origin	Type of reproduction	Seed dispersal mode	Vegetative dispersal mode	Growth form	References
CORE EUDICOTS									
Poaceae	*Deschampsia antarctica*	Circumpolar	3	Auto.	SV	Ane + Zoo	Ane + Zoo + Clo	Tu	Cour (1958); Aubert de la Rüe (1964); Convey (1996); Frenot et al. (2001)
	Festuca contracta	Circumpolar	3	Auto.	SV	Ane	Ane + Clo	Tu	Aubert de la Rüe (1964); Tallowin & Smith (1977); Frenot et al. (2001)
	Poa annua	Worldwide	5	Intr.	SV	Ane + Hyd + Zoo	Clo	Tu	Frenot et al. (2001); Durka (2002); Kleyer et al. (2008)
	Poa cookii	Crozet Is., Marion I., Kerguelen Is., Heard I., Edward I., McDonald I., Macquarie I.	2	Auto.	SV	Ane	Ane + Clo	Tu	Lourteig & Cour (1963); Hennion & Walton (1997b); Frenot et al. (2001)
	Poa kerguelensis	Kerguelen Is., Heard I.	1	Auto.	SV	Ane	Ane + Clo	Tu	Lourteig & Cour (1963); Hennion & Walton (1997b); Frenot et al. (2001)
Ranunculaceae	*Ranunculus biternatus*	Circumpolar	3	Auto.	SV	Hyd + Zoo	Hyd + Zoo + Clo	Ro	Lourteig & Cour (1963); Hennion & Walton (1997b); Frenot et al. (2001)
Caryophyllaceae	*Colobanthus kerguelensis*	Kerguelen Is.; Heard I.	1	Auto.	SV	Hyd	Clo	Cu + Ro	Lourteig & Cour (1963); Hennion & Walton (1997b); Frenot et al. (2001)
	Sagina procumbens	Worldwide	5	Intr.	S	Ane + Hyd + Zoo	No	Cu + Ro	Frenot et al. (2001); Durka (2002); Pakeman et al. (2002); Kleyer et al. (2008)
Portulacaceae	*Lyallia kerguelensis*	Kerguelen Is.	1	Auto.	S	Hyd	No	Cu	Lourteig & Cour (1963); Hennion & Walton (1997b); Frenot et al. (2001)
	Montia fontana	Worldwide	5	Auto.	SV	Ane + Hyd + Zoo	Clo	Br	Frenot et al. (2001); Durka (2002); Kleyer et al. (2008)
Rosaceae	*Acaena magellanica*	Austral	4	Auto.	SV	Ane + Zoo	Clo	Br + Ro	Chastain (1958); Walton (1979); Frenot et al. (2001); Chapuis et al. (2004)
Brassicaceae	*Pringlea antiscorbutica*	Crozet Is., Kerguelen Is., Marion I., Heard I., Edward I., McDonald I.	1	Auto.	S	Ane + Hyd	No	Ro	Lourteig & Cour (1963); Frenot et al. (2001); Schermann-Legionnet et al. (2007)
Asteraceae	*Senecio vulgare*	Worldwide	5	Intr.	S	Ane + Hyd + Zoo	No	Ro	Frenot et al. (2001); Durka (2002); Robinson et al. (2003); Kleyer et al. (2008)
	Taraxacum erythrospermum	Worldwide	5	Intr.	S	Ane + Hyd + Zoo	No	Ro	Frenot et al. (2001); Durka (2002); Kleyer et al. (2008)

III.3. Phenotypic and environmental sampling

On each sampling point, we selected five individual plants of each species present. Sampling was limited to this number of individuals because of the sparse vegetation in some sites. A more extended sampling would have involved working in a larger area in which environmental conditions were not homogeneous. We chose robust and well-grown plants. We excluded plants strongly affected by herbivores or pathogens. We selected plants in average environmental conditions at the sampling point (e.g. average wind exposure).

On each selected individual, we then measured the plant height, the plant diameter and the length of the largest leaf as indicators of plant size. We did not measure length of the largest leaf on *Lyallia kerguelensis* which have small, coriaceous and densely imbricated leaves, thus not informative for plant size. We performed measurements of plant height and plant diameter appropriately to the growth form of each plant species (Appendix II.S1). We also recorded the most advanced flowering stage as indicator of the plant reproductive stage (Appendix II.S2).

We measured altitude, moisture and salinity at each sampling point. We determined altitude with a GPS. We collected five soil samples around the measured plants at each sampling point. The first half of each soil sample was dried at 60°C to constant weight to determine relative water content. We determined pore water conductivity as described in Appendix II.S3. We finally calculated the mean conductivity and the mean moisture across the five soil samples at each sampling point.

III.4. Data analyses

III.4.1. Mean phenotype and phenotypic variability

At each sampling point and for each species, we calculated the mean values of the four traits across the five measured plants. We then calculated the mean values of the four traits across all of the sampling points in order to characterize the mean phenotype of each species within the

study area. We also calculated coefficients of variation (CV = ratio standard deviation / mean) of the four measured traits in order to quantify the phenotypic variability of each species within the study area. We used the CV of plant traits because the standard deviation among attributes of the four traits increased with their mean. The mean trait values and the CV of the four traits were regressed against the endemism level of species using Spearman rank correlation analyses (StatSoft 2010). This non-parametric statistical method was convenient because the set of mean trait values and trait CV across species did not follow a normal distribution and because sample sizes differed between the species.

III.4.2. Mean environmental position and variability

To characterize the mean environmental position of each species along each of the three environmental gradients, we calculated the mean altitude, mean conductivity and mean moisture across all of the sampling points where that species occurred. To quantify the environmental variability of each species along each of the three environmental gradients, we calculated CV of altitude and salinity and standard deviation of moisture. We did not use CV of moisture because the standard deviation of this environmental variable was independent of its mean. As above, the mean positions and variance of species along each of the three environmental gradients were regressed against the species endemism level using Spearman rank correlation analyses.

III.4.3. Phenotypic and environmental integration

To quantify the phenotypic integration of each species within the study area, we ran a separate principal component analysis (PCA) which included all of the traits measured for that species. The percentage of variance explained by the first axis of the PCA (PCA1) reflected the strength of correlations between traits. The higher the percentage of variance captured by the PCA1, the

higher the phenotypic integration of the species was. To examine in detail phenotypic integration within species, plant traits were correlated one to each other by using simple linear regressions. For each regression, we calculated the effect size as a Fisher coefficient Zr from the correlation coefficient in order to quantify the strength of the trait correlation (Rosenthal 1984). The PCA1 and the Fisher coefficient Zr of species were regressed against their level of endemism using Spearman rank correlation analyses. We applied the same approach to study the environmental integration.

III.4.4. Correlations between traits and abiotic variables

As trait variables and environmental variables are both intercorrelated, we first examined correlation between traits and abiotic variables using for each species a linear regression between a composite phenotypic variable (coordinates on PCA1 of the four trait variables) and a composite environmental variable (coordinates on PCA1 of the three abiotic variables). As above, we calculated the effect size as a Fisher coefficient Zr for each regression. As a given species may employ fundamentally different morphological and physiological strategies to respond to different environmental gradients, in a second time we examined the univariate relationships between traits and abiotic variables. Plant traits were regressed against environmental variables using simple linear and quadratic regressions. We chose to perform linear and quadratic regressions because they are the more commonly observed relationships between traits and environmental gradients. For each correlation, we selected the best regression model (linear or quadratic) from the higher determination coefficient (R^2). We then calculated the effect size as a Fisher coefficient Zr of the selected regression model as above. For each species, we obtained twelve effect sizes from the simple regressions between the four traits and the three abiotic variables. Finally, we examined relationships between endemism level of species and (i) the effect sizes from the regression between coordinates on PCA1 of

traits and coordinates on PCA1 of environmental variables, (ii) the twelve effect sizes from the simple regressions between traits and abiotic variables and (iii) the mean across the twelve effect sizes, using Spearman rank correlation analyses.

III.4.5. Phylogenetic positions, origins and life-histories of species

To verify whether observed significant patterns depended on the phylogenetic positions of the species, we examined relationships between the phenotypic and environmental characteristics and the endemism level within each studied family. Except the Ranunculaceae, Brassicaceae and Roasaceae, the families were represented by at least two species which differed in their endemism level (Fig. II.3). We grouped Brassicaceae and Rosaceae as they belong to the same order (Rosales). As the number of species within each family (or group of families) and the number of families were small, we could not perform statistical tests. We qualitatively verified whether the same trends as the observed relationships (i.e. sign of the relationships with level of endemism) were found within most of the families. We applied the same approach to verify whether observed relationships depended on the life histories of the species (i.e. growth form, seed dispersal mode, vegetative dispersal mode and type of reproduction, Fig. II.3). We did not apply the same approach to verify the influence of the origin of species on the observed relationships, as all of the introduced species had a widespread distribution in our study (i.e. they all belonged to the endemism level 5). We thus only verified whether the same trends as the observed relationships were found among the autochthonous species.

IV. Results

IV.1. Phenotypic and environmental mean values and variabilities

Results on relationships between endemism level of species and their phenotypic and environmental mean values and variabilities are given in Table II.1. We found that mean values

of the four traits did not vary between species with different endemism levels, and neither did the coefficients of variation of the four traits. Similarly, we found that mean positions and variation of species along the moisture gradient did not significantly vary with their level of endemism, and so was the coefficient of variation of salinity. Conversely, we found a significant relationship between the mean position of species along the salinity gradient and their level of endemism: endemics occupied lower positions along the salinity gradient. Finally, mean position and variation of species along altitudinal gradient highly significantly differed with their level of endemism: endemics occupied higher and less variable positions along the altitudinal gradient.

Table II.1 Spearman rank correlations between endemism level of species and their mean phenotype (mean values of the four traits), their phenotypic variability (CV of the four traits), their mean position along the three environmental gradients (mean values of the three environmental variables), their variation along the three environmental gradients (CV of altitude and salinity and standard deviation of moisture). n = 14, except for length of the biggest leaf where n = 13 because it was not measured for *Lyallia kerguelensis*. The Spearman rank correlation coefficient is given. NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Mean		Variability	
Traits				
Plant height (cm)	0.00	NS	0.17	NS
Plant diameter (cm)	-0.15	NS	-0.12	NS
Length of the largest leaf (cm)	-0.17	NS	0.03	NS
Flowering stage	0.43	NS	-0.42	NS
Environments				
Altitude (m)	-0.88	***	0.72	**
Moisture (%)	0.45	NS	0.00	NS
Salinity (µS/cm)	0.56	*	0.33	NS

IV.2. Phenotypic integration

The percentage of variance explained by the first axis of the PCA across the four traits highly significantly increased with the endemism level of species (Fig. II.4a). The effect sizes from the simple regressions between traits showed the same trends: they increased with the endemism level of species (Appendix II.S4). However, the simple regression between plant height and plant diameter was the only one to significantly increase with endemism level (Spearman rank

correlation, n = 14; r = -0.70; p = 0.006). The five other simple regressions between traits did not significantly increase with the endemism level of species (Spearman rank correlations, n = 13 – 14; r = -0.27 – -0.37; p = 0.11 – 0.35).

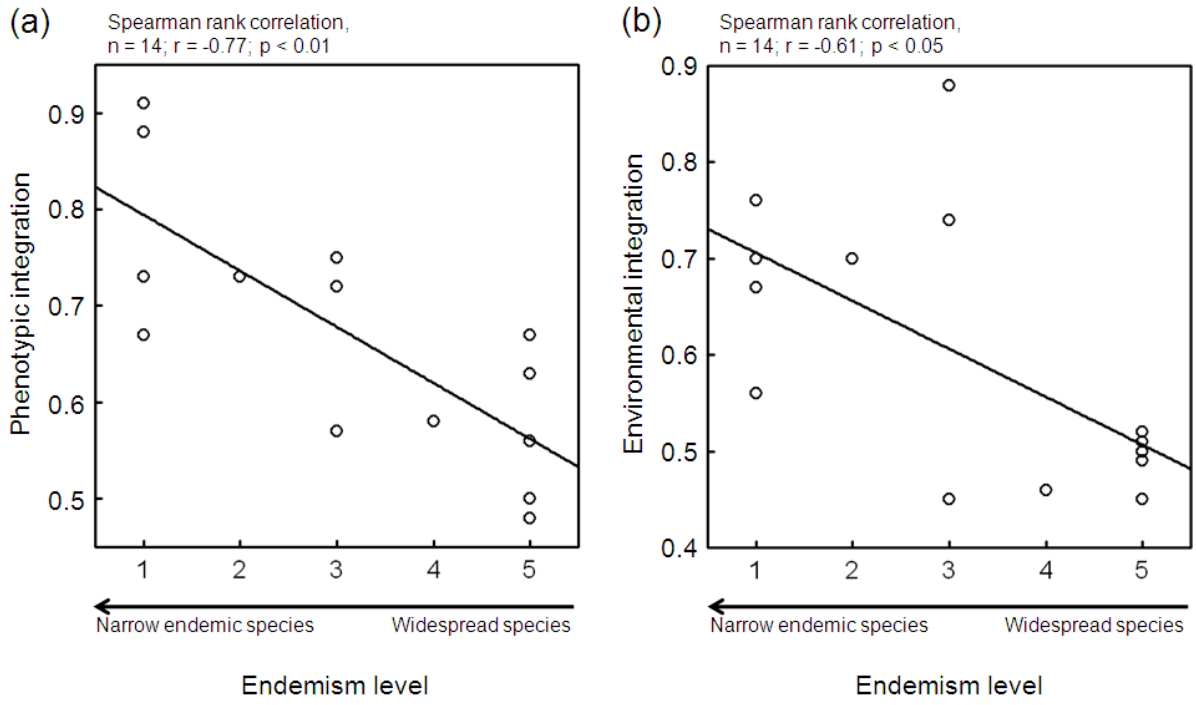

Figure II.4 Relationship between (a) phenotypic integration of species and their level of endemism and between (b) environmental integration of species and their level of endemism. In this Figure, phenotypic integration was the percentage of variance explained by the first axis of the PCA which included all of the traits measured for a species. Environmental integration was the percentage of variance explained by the first axis of the PCA which included all of the abiotic measurements for a species. Endemism level of species was determinate according to their geographical distribution (see Methods).

IV.3. Environmental integration

The percentage of variance explained by the first axis of the PCA across the three environmental variables significantly increased with the endemism level of species (Fig. II.4b). The study of the effect sizes from the simple regressions between environmental variables gave the same conclusions: they increased with the endemism level of species (Appendix II.S4). More precisely, the correlation between altitude and salinity significantly increased with endemism level of species (Spearman rank correlation, n = 14; r = -0.55; p = 0.04), and so was

the correlation between moisture and salinity (Spearman rank correlation, n = 14; r = -0.55; p = 0.04). Conversely, the correlation between altitude and moisture did not significantly increase with the endemism level of species (Spearman rank correlation, n = 14; r = -0.37; p = 0.19).

IV.4. Correlations between traits and abiotic environment

The effect sizes from the regression between the coordinates on PCA1 of traits and the coordinates of PCA1 of environmental variables highly significantly increased with the endemism level of species (Fig. II.5). The univariate analyses brought the same conclusions (Appendix II.S4). The twelve effect sizes from the simple regressions between traits and abiotic variables increased with the endemism level, five of them significantly (Spearman rank correlations; n = 13 – 14; r = -0.12 – -0.65; p = 0.02 – 0.68). We also found a significant increase with the endemism level of species in the means across the twelve effect sizes (Spearman rank correlation, n = 14; r = -0.77; p = 0.003).

IV.5. Phylogenetic positions, origins and life-histories of species

The observed significant relationships between the endemism level of species and their environmental positions and variabilities, phenotypic integration, environmental integration and strength of correlations between traits and environments did not depend on phylogenetic positions, origins and reproductive modes of species (Appendix II.S5). More precisely, we found the same trends as the observed relationships within all of the studied families, within the autochthonous species and for both vegetative and sexual reproductive modes. We also found the same trends as the observed relationships within most of the growth forms and the vegetative dispersal modes, except some minor relationships which tended to be positively related to endemism level within the rosette species and within both anemochorous and clonal vegetative dispersal mode. Interestingly, several of the observed patterns seemed to depend on

the seed dispersal mode: the relationships tended to be positively related to endemism level within the anemochorous species and within the both anemochorous, hydrochorous and zoochorous species.

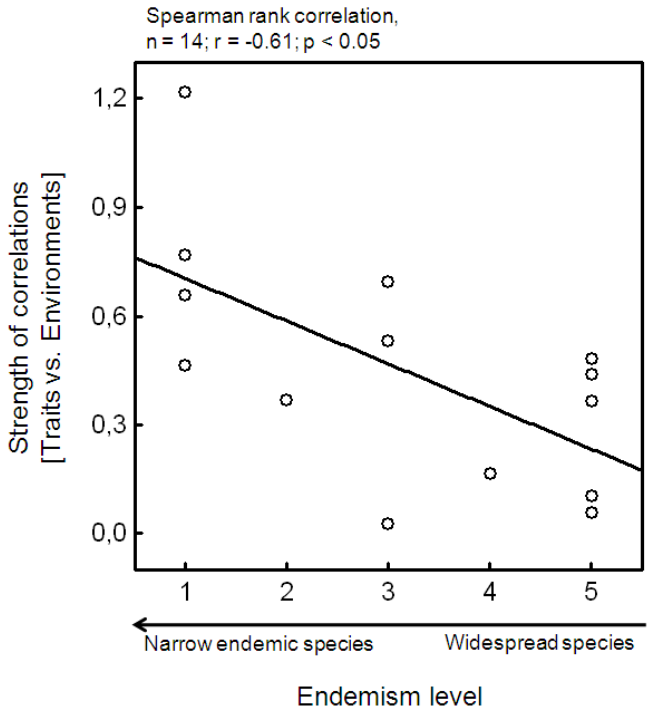

Figure II.5 Relationship between the strength of the correlations [traits vs. environments] and the endemism level of species. In this Figure, strength of the correlations [traits vs. environments] of a species was the effect size from simple linear regression between a composite phenotypic variable (coordinates on the PCA1 of the four trait variables) and a composite environmental variable (coordinates on the PCA1 of the three abiotic variables). Endemism level of species was determinate according to their geographical distribution (see Methods).

V. Discussion

This study combined geographical distribution data and phenotypic and environmental field measurements for fourteen plant species growing in the sub-Antarctic Kerguelen Islands. We found that mean trait values and variabilities of species were independent of their level of endemism. Moreover, endemic species occupied higher and less variable positions along the altitudinal gradient and lower positions along the salinity gradient. Finally, we showed for the first time an increase in phenotypic integration, environmental integration and

trait/environment correlations with the endemism level of species. These results suggested that species with higher endemism levels may be constrained to particular combinations of environmental conditions, where they may only exhibit some particular combinations of phenotypic traits. Ultimately, these high phenotypic and environmental integrations may result in strong correlations between traits and environments. These patterns were independent from either phylogenetic position or origin of species, but may depend on their growth form and dispersal modes.

The integration within and between phenotypes and environments increased with the endemism level of species. This suggested a particular specialization of endemic species to the sub-Antarctic environmental conditions. This finding supports the hypothesis of an old history of endemic species in the sub-Antarctic region. Our results are consistent with a case of endemism that would result from the increasing restriction of the species habitat over time (paleoendemism, Stebbins & Major 1965). The successive glaciations since the Oligocene in the Antarctic resulted in an important restriction of viable habitats for terrestrial biotas and caused mass extinctions in the Antarctic flora (Ashworth & Cantrill 2004). Recent progress both in glaciological modeling and in molecular phylogenetic and phylogeographic tools have revealed a much more frequent occurrence in the Antarctic continent of persistence of species in ice-free locations (nunataks) than was previously believed, demonstrating cases of paleoendemism there (Convey et al. 2008, 2009). In the sub-Antarctic, recent geological and paleobotanical information and large-scale analyses of present-day vegetation provided strong presumption for the survival of the autochthonous sub-Antarctic phanerogamic flora in local refugia during the last ice age (Van der Putten et al. 2010). More phylogenetic data on autochthonous plant species will be needed for understanding their origin and dating their colonization in the Kerguelen Islands (Wagstaff & Hennion 2007). Recent work however allowed proposing that the strict Kerguelen endemic *Lyallia kerguelensis*, evolved from an

Antarctic ancestor, would have dispersed and survived on the milder Kerguelen during major Antarctic cooling while ancestors became extinct on the continent (Wagstaff & Hennion 2007). Therefore, other plant species may also have survived in narrow ice–free habitats in Kerguelen and become endemic to this province with a few surrounding islands. Our results provide strong ecological arguments supporting the paleoendemism hypothesis for the geographically restricted phanerogams of the sub-Antarctic flora.

Our results also suggested that the more endemic species are, the stronger they are constrained in phenotypes and environments. Endemic species may thus not have the sufficient phenotypic flexibility to disperse outside their specific habitats. This is consistent with the hypothesis that endemic species are specialists to particular ecological conditions (Stebbins 1980), where they maximize performance (survival and reproduction), but are unable to occupy other environments (Caley & Munday 2003). Conversely, widespread species may cope with a wider range of environments, with a decline in performance in each environment (Sultan et al. 1998; Richards et al. 2005). There are some evidences for such trade-offs in the autochthonous sub-Antarctic flora. All of the endemic species to the Southern Indian Ocean Province (except *Lyallia kerguelensis*) show a regular and relatively high production of viable seeds and share rapid development and early seed ripening, a phenology that was considered opportunistic and adaptive to a harsh climate (Hennion et al. 2006b). In contrast, some other autochthonous, non endemic species encounter limitations in seed fertility in sub-Antarctic islands (Hennion et al. 2006b). Among the more endemic species, the Brassicaceae *Pringlea antiscorbutica* that was particularly well studied clearly displays specific adaptations to sub-Antarctic abiotic conditions. In the field in Kerguelen, photosynthesis is sustained throughout the year even at temperatures close to 0°C, and growth and development occur without a period of dormancy (Aubert et al. 1999). Cultivation under temperate conditions results in rapid plant death (Hennion et al. 2006b). In seedlings, both root and shoot growth require cold temperature (5°C

night/10°C day) as soon as germination is completed (Hummel et al. 2002, Dufeu et al. 2003). Strong heat, salt or drought stresses resulted in high seedling mortality with dramatic changes in the balance of growth regulators polyamines, all this suggesting that *P. antiscorbutica* may not have the physiological ability to cope with large changes in abiotic conditions (Dufeu et al. 2003, Hummel et al. 2004). Moreover, our recent ecological study on *Pringlea antiscorbutica* indicated that the strong phenotypic integration in this species may limit its flexibility in reproductive strategies and may constrain its distribution towards higher altitudes (Hermant et al. submitted). This species seems to maximize its reproductive performance within its present altitudinal range and is unlikely to be able to disperse to a larger range.

We found that the more endemic the species were; the higher and less variable positions they occupied along the altitudinal gradient, corresponding in Kerguelen to more stressful and competition-free conditions. Restriction of endemic species to high altitudes may indicate that species are limited to these stressful habitats in order to escape from the inter-specific competition at low altitude. This hypothesis was already proposed for the endemic species *Arctostaphylos myrtifolia* in the central Sierra Nevada foothills of California (Gankin & Major 1964) and for the Mediterranean endemic flora (Lavergne et al. 2003, 2004). In Kerguelen, this hypothesis was supported by the stress tolerance, the low competitiveness and the low dispersal ability of some endemic species. For example, the strict endemic species *Lyallia kerguelensis* is found in very exposed but humid places, such as wind corridors with frequent frost, growing on gravel, moraine deposits or syenites (Wagstaff & Hennion 2007). This species was already described as "very local" and appears to hardly colonize new areas (Wagstaff & Hennion 2007). *L. kerguelensis* shows poor germination and little seed dispersal (Hennion 1992; Hennion & Walton 1997b). As a whole, the traits of *L. kerguelensis* suggest that this species may be unlikely to compete successfully with autochthonous or introduced species linked with climate change (Wagstaff & Hennion 2007). The sub-Antarctic cushion plant *Azorella selago*

(Apiaceae) is another slow colonizer (Frenot et al. 1998), although it is geographically much more widely distributed than *Lyallia*. Finally, *Pringlea antiscorbutica* and *Poa cookii* are tolerant to some salt exposure in coastal sites at low altitudes, where competition is low (Pammenter & Smith 1983; Hennion & Bouchereau 1998; Chapuis et al. 2000). Our results and these overall observations on ecological and biological characteristics of the sub-Antarctic endemic species provide several lines of evidence for the hypothesis that endemic species may be limited to stressful habitats in order to escape interspecific competition.

The observed relationships with phenotypic and environmental integration may differ according to the dispersal modes of species. In Kerguelen, the endemic and circumpolar species are dispersed by wind and/or freshwater, while austral and cosmopolitan species are dispersed by wind and animals (Chastain 1958; Tallowin & Smith 1977; Convey 1996; Hennion & Walton 1997b; Durka 2002; Pakeman et al. 2002; Robinson et al. 2003; Chapuis et al. 2004; Schermann et al. 2007; Kleyer et al. 2008, Fig. II.3). This unequal distribution of the dispersal modes across the level of endemism may explain why some of the observed relationships were lost within each dispersal mode. It may also indicate that the dispersal mode is a factor that contributes to the geographic distribution of angiosperm species in the Southern Hemisphere. The ability to disperse by seeds is evident within Kerguelen archipelago for *P. antiscorbutica*, *C. kerguelensis*, *Ranunculus moseleyi*, *P. kerguelensis*, and *P. cookii* (Hennion & Walton 1997a). The presence of all of these species in other islands of the Southern Indian Ocean Province, plus Macquarie Island for *Poa cookii*, being all islands of volcanic origins, implies their dispersal at some distance and even very long distance for the latter. To this regard, it is of particular interest that the species that shows the lowest potential of long-distance dispersal, namely *Lyallia kerguelensis*, is also the most restricted in its geographical distribution (Hennion & Walton 1997a). Conversely, there is some evidence for long distance dispersal by seabirds for some of the more widespread species, such as *Ranunculus biternatus*, *Acaena*

magellanica and *Poa annua* (Scott 1989; Hennion & Walton 1997a; Chapuis et al. 2004). Recent studies have shown strong provincialism in the present-day antarctic and sub-Antarctic biotas, suggesting long-term persistence of species, rather than recent colonization (Convey et al. 2009; Van der Putten 2010). As a whole, the dispersal of propagules between sub-Antarctic Islands remains largely unknown nowadays. Investigating this process through a thorough study of vectors, including birds, may constitute one of the future challenges for biological research in this region.

Our patterns on phenotypic integration, environmental integration and trait/environment correlations tended to be stronger when they were examined through a multivariate approach. This indicated that phenotypic responses of plants to environmental variations are likely to be complex and multivariate (Richards et al. 2005) and underscored the importance to account for multiple interactions within and between phenotypes and environments.

Our finding that endemic species are restricted to particular combinations of environmental conditions may have strong implications under the present climate change in the sub-Antarctic region (Bergstrom & Chown 1999), in particular in Kerguelen (Frenot et al. 2006). A high sensitivity to dry conditions was already observed in several endemic species and their low ability to cope with environmental changes was suggested (Hennion 1992; Chapuis et al. 2004; Hummel et al. 2004). Our results suggest that this particular sensitivity of endemic species to climate change may be due to disappearance of the environmental combinations where the endemic species specifically occur. This may ultimately lead endemic species to extinction. This has major implications for the conservation of the sub-Antarctic flora under the rapid climate change in this region.

VI. Conclusion

This study related phenotypic and environmental integration of fourteen plant species from the Kerguelen Islands to their level of endemism. Overall, we found that species with higher endemism levels were more integrated within and between phenotypes and environments and were in average restricted to the higher altitudes. Our results suggest a long-term specialization of endemic species to particularly stressful and competition-free habitats, supporting a scenario of paleoendemism. However, this strong integration may limit the flexibility of endemic species to respond to novel environmental conditions, especially to the present climate change in the sub-Antarctic region.

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IX. Supporting information

Appendix II.S1 Measurements of plant height and plant diameter appropriately to the growth form of each plant species.

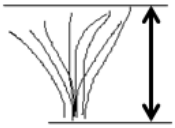
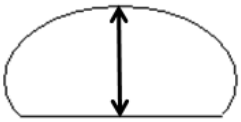
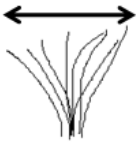
Appendix II.S2 Flowering stages.

Appendix II.S3 Measurements in laboratory of soil moisture and conductivity.

Appendix II.S4 Spearman rank correlations between endemism level of species and the effect sizes (Fisher coefficient Zr) from the twelve simple regressions between the four measured traits and the three abiotic variables.

Appendix II.S5 Effect of phylogenetic positions, life-histories and biogeographical origins of species on the observed significant relationships between endemism level of species and their environmental position and variation, phenotypic integration, environmental integration and strength of correlations between traits and environments.

Appendix II.S1 Measurements of plant height and plant diameter appropriately to the growth form of each plant species.

	TUFT	CUSHION	ROSETTE	BRANCHED
HEIGHT	 Height from the ground to the extremity of the higher leaf	 Maximal height	 Height from the ground to the extremity of the higher leaf	 Length from the base of the branch to the extremity of the sub-apical leaf
DIAMETER	 Maximal diameter	 Maximal diameter	 Maximal diameter of the rosette	 Maximal diameter of the branch including the leaves
SPECIES	- *Deschampsia antarctica*, - *Festuca contracta*, - *Poa annua*, - *Poa cookii*, - *Poa kerguelensis*	- *Colobanthus kerguelensis*, - *Lyallia kerguelensis*, - *Sagina procumbens* (dense cushion)	- *Acaena magellanica* (isolated individual) - *Pringlea antiscorbutica*, - *Ranunculus biternatus*, - *Sagina procumbens* (rosette plant) - *Senecio vulgaris*, - *Taraxacum erythrospermum*	- *Acaena magellanica* (vegetative cover) - *Montia fontana*

Appendix II.S2 Flowering stages

Stage	Corresponding biological state
0	No buds: meristem in vegetative stage or in the initial stage of flowering
1	Young buds: all organs are formed
2	Mature buds
3	Flower opening: young flower, reproductive organs are not mature
4	Fecundation: mature flower, triggering of anthers dehiscence, receptive stigmas
5	Flower fading: empty anthers, fecund carpels begin to growth
6	Seeds developing
7	Mature seeds

Appendix II.S3 Measurements in laboratory of soil moisture and conductivity

Evaluation of soil humidity

- Put about half of the soil sample in a container and weigh the fresh mass, Wf_1 (in g).
- Put the container in the oven or the incubator. Dry at 60°C for at least 60h.
- Remove the container from the incubator and immediately weigh the dry mass Wd_1 (in g).
- Soil humidity is calculated using the following equation:

  Water content (%) = 100 x (Wf_1 – Wd_1) / Wd_1.

Measure of conductivity

- Weigh the fresh mass Wf_2 of the second half of the soil sample
- The soil dry mass Wd_2 is evaluated using the following equation:

  Wd_2 = (1 – Water content / 100) x Wf_2
- Estimate the quantity of water Qs in this soil using the following equation:

  Qs = Wd_2 x (Water content / 100).
- Add a known volume Qw of distilled water to the sample in order to obtain a supernatant. Calculate the dilution factor F using the following equation: F = (Qs + Qw) / Wd_2.
- Once the water is added, vortex the tubes for 2 minutes. Wait at least 15 minutes. Vortex each tube again for 30 s. Let it rest for 18 to 24h.
- Calibrate the electrical conductivity meter with a KCl calibration solution of 1413 µS.
- As the conductivity is sensitive to temperature, measure the conductivity in a heated room at 25°C. Dip the conductivity meter electrode in the clear solution above the sediments, and measure the conductivity C_{obs}.
- Correct the conductivity measure by the dilution factor: C = C_{obs} x F

Appendix II.S4 Spearman rank correlations between endemism level of species and the effect sizes (Fisher coefficient Zr) from the twelve simple regressions between the four measured traits and the three abiotic variables.

	Plant height	Plant diameter	Length of the biggest leaf	Flowering stage	Altitude	Moisture	Salinity
Plant height		-0.70 **	-0.37 NS	-0.32 NS	-0.62 *	-0.52 NS	-0.37 NS
Plant diameter			-0.47 NS	-0.27 NS	-0.44 NS	-0.12 NS	-0.58 *
Length of the biggest leaf				-0.28 NS	-0.32 NS	-0.60 *	-0.56 *
Flowering stage					-0.65 *	-0.21 NS	-0.24 NS
Altitude						-0.37 NS	-0.55 *
Moisture							-0.55 *
Salinity							

Sample size n = 14, except for length of the biggest leaf where n = 13 because it was not measured for *Lyallia kerguelensis*. The Spearman rank correlation coefficient is given. NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Appendix II.S5 Effect of phylogenetic positions, life-histories and biogeographical origins of species on the observed significant relationships between endemism level of species and their environmental position and variation, phenotypic integration, environmental integration and strength of correlations between traits and environments.

(a) Signs of the relationships between endemism level of species and their environmental position and variation, phenotypic integration, environmental integration and strength of correlations between traits and environments within each family (or group of families).

	Global pattern	Asteraceae	Caryophyllaceae	Poaceae	Portulacaceae	Rosaceae - Brassicaceae
Environmental position and variation						
Mean altitude	-	-	-	-	-	-
Mean salinity	+	+	+	+	+	+
Coefficient of variance of altitude	+	+	+	+	+	+
Phenotypic integration						
Variance on PCA1 of all the traits	-	-	-	-	-	-
Zr [plant height vs. plant diameter]	-	-	-	-	-	-
Environmental integration						
Variance on PCA1 of all the abiotic variables	-	-	-	-	-	-
Zr [altitude vs. salinity]	-	-	-	-	+	-
Zr [moisture vs. salinity]	-	-	-	-	-	-
Correlations [traits vs. environments]						
Zr [PCA1 of traits vs. PCA1 of abiotic variables]	-	-	-	-	-	-
Mean Zr [traits vs. abiotic variables]	-	-	-	-	-	-
Zr [plant height vs. altitude]	-	-	-	-	-	-
Zr [plant diameter vs. salinity]	-	-	-	-	-	+
Zr [length of the biggest leaf vs. moisture]	-	-	-	-		-
Zr [length of the biggest leaf vs. salinity]	-	-	-	-		-
Zr [flowering stage vs. altitude]	-	-	-	-	-	-

(b) Signs of the relationships between endemism level of species and their environmental position and variation, phenotypic integration, environmental integration and strength of correlations between traits and environments within each life-history (types of reproduction, seed dispersal modes, vegetative dispersal modes and growth-forms). Types of reproduction are S: by seed; SV: by seed and vegetatively. Dispersal modes are Ane: anemochorous; Hyd: hydrochorous; Zoo: zoochorous; and Clo: clonal. Growth forms are Cu: cushion; Br: branched; Ro: rosette; Tu: tuft.

	Global pattern	Type of reproduction		Seed dispersal modes			Vegetative dispersal modes			Growth modes			
		S	SV	Ane	Hyd and Ane + Hyd	Ane + Hyd + Zoo	Clo	Ane + Clo	No	Tu	Ro	Cu and Cu + Ro	Br and Br + Ro
Environmental position and variation													
Mean altitude	-	-	-	-	-	-	-	-	-	-	-	-	-
Mean salinity	+	+	+	+	+	-	+	+	+	+	+	+	+
Coefficient of variance of altitude	+	+	+	+	+	-	+	+	+	+	+	+	+
Phenotypic integration													
Variance on PCA1 of all the traits	-	-	-	+	-	-	-	+	-	-	-	-	-
Zr [plant height vs. plant diameter]	-	-	-	-	-	+	-	-	-	-	-	-	-
Environmental integration													
Variance on PCA1 of all the abiotic variables	-	-	-	-	-	-	-	-	-	-	-	-	-
Zr [altitude vs. salinity]	-	-	-	-	-	-	-	-	-	-	-	-	-
Zr [moisture vs. salinity]	-	-	-	+	-	-	-	+	-	-	-	-	-
Correlations [traits vs. environments]													
Zr [PCA1 of traits vs. PCA1 of abiotic variables]	-	-	-	-	-	-	-	-	-	-	+	-	-
Mean Zr [traits vs. abiotic variables]	-	-	-	-	-	-	-	-	-	-	-	-	-
Zr [plant height vs. altitude]	-	-	-	-	-	-	-	-	-	-	-	-	-
Zr [plant diameter vs. salinity]	-	-	-	+	-	-	-	+	-	-	-	-	+
Zr [length of the biggest leaf vs. moisture]	-	-	-	-	-	-	-	-	-	-	+	-	-
Zr [length of the biggest leaf vs. salinity]	-	-	-	-	-	-	-	-	-	-	-	-	-
Zr [flowering stage vs. altitude]	-	-	-	-	-	-	-	-	-	-	+	-	-

(c) Signs of the relationships between endemism level of species and their environmental position and variation, phenotypic integration, environmental integration and strength of correlations between traits and environments within the ten autochthonous species.

	Global pattern (autochthonous and introduced species)	Autochthonous species
Environmental position and variation		
Mean altitude	-	-
Mean salinity	+	+
Coefficient of variance of altitude	+	+
Phenotypic integration		
Variance on PCA1 of all the traits	-	-
Zr [plant height vs. plant diameter]	-	-
Environmental integration		
Variance on PCA1 of all the abiotic variables	-	-
Zr [altitude vs. salinity]	-	-
Zr [moisture vs. salinity]	-	-
Correlations [traits vs. environments]		
Zr [PCA1 of traits vs. PCA1 of abiotic variables]	-	-
Mean Zr [traits vs. abiotic variables]	-	-
Zr [plant height vs. altitude]	-	-
Zr [plant diameter vs. salinity]	-	-
Zr [length of the biggest leaf vs. moisture]	-	-
Zr [length of the biggest leaf vs. salinity]	-	-
Zr [flowering stage vs. altitude]	-	-

Chapitre III

Disparate relatives: life histories vary more in genera occupying intermediate environments

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En préparation

Disparate relatives: life histories vary more in genera occupying intermediate environments

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I. Abstract

Species within clades are commonly assumed to share similar life histories traits, but within a given region some clades show much greater variability in traits than others. Are variable clades older and had more time for trait diversification? Or do variable clades occupy particular environments providing diverse opportunities permitting the establishment and maintenance of diverse trait states? Does environmental opportunity operate across all species of the species pool, or is it specific to species belonging to the same clade, increasing only within-clade trait variability? We studied the variability of six life-history traits within >700 angiosperm genera in Central Europe, distributed along six abiotic gradients. We found that trait variability differed strongly between genera, but did not depend on their age. Trait variability was higher in genera occupying intermediate position along abiotic environmental gradients, contrary to patterns established across the regional species pool (and unbiased by geographical sampling, family membership or species richness). Increasing trait variability within genera reflected increasing independency of traits from the abiotic environment, possibly due to more diverse biotic interactions. Overall, we suggest that trait variability depends on ecological processes specific to clades: intermediate abiotic environments may play an important role in generating and maintaining the amazing diversity of life histories realized within certain clades.

Key-words: Angiosperms, abiotic environmental gradients, clades, life-history traits, dated phylogeny, trait variability.

II. Introduction

Clades within a region differ in their species richness but also their trait variability, and high species richness does not equal high trait variability (Losos & Miles 2002; Adams *et al.* 2009). The trait variability, or functional diversity, realized within a clade can for instance be measured as the standard deviation of attributes of a given trait across its constituent species. High variability of traits in some clades may undermine the common tenet that clades can be used as a proxy for traits (Webb et al. 2002). While the factors driving species diversity of clades within a region have been extensively studied (e.g. Bowker et al. 2010; Kozak & Wiens 2010), those driving the trait variability within clades are much less known. It has been suggested that increased present-day trait variability within some clades might be due to larger age of these clades providing more time to diverge in traits (Moles et al. 2005; Ackerly & Nyffeler 2004; Fig. III.1a). But, increased present-day trait variability within clades may also depend on the environments occupied by the clades' constituent species. We know that local ecological interactions or environmental filters may affect both the diversity of clades and of traits realized within local communities (e.g. Helmus et al. 2007a), but we do not know whether across an entire region, clades occupying particular environments show more variable traits than clades occupying different other environments.

Environments may influence the trait diversity of their entire species pool (Stevens et al. 2003; Ackerly & Cornwell 2007). Particular types of environments may provide a particularly wide range of abiotic or biotic opportunities for assemblage of species that differ strongly in traits (Fig. III.1b). These particular environments might hence promote the establishment and maintenance of a particularly large variability of trait states within the corresponding species pools. Clades occupying these particular types of environments (Prinzing et al. 2001) may reflect the increased trait variability of the corresponding species pools. Environmental opportunity, however, does not necessarily operate across all species of the species pool; it

might be specific to species belonging to the same clade, increasing only within-clade trait variability (Fig. III.1c). For instance, particular environments may provide many closely related competitors, or many phytophages or pollinators specialized on a given incumbent plant clade (DiMichele et al. 2004; Pfennig 2009). Interactions with these species will promote the establishment and maintenance of a particularly large variability of trait states within each clade occupying these environments, without increasing trait variability of the entire environmental species pools (for possible consequences on local coexistence see for instance Helmus et al. 2007a; Swenson & Enquist 2007; Gomez et al. 2010).

Some of the best studied factors that influence plant traits are abiotic stress (e.g. frost) and competitive interactions (Grime 1977). These factors may vary inversely across most abiotic gradients, as abiotic stress is suggested to become more intense and competitive interactions less important towards extremities of gradients (Welden & Slauson, 1986). Also, the sheer number of potentially interacting species is considered to declines towards the extremes (Michalet et al. 2006; Bartish et al. 2010). Both, abiotic stress and competition (and other biotic interactions) may influence trait variability through strong directional selection pressures (Swenson & Enquist 2007; Pfennig 2009) as well as through strong ecological sorting (Helmus et al. 2007a). Overall, if environment influence trait variability within genera, we may expect that trait variability becomes either more important or less important towards the extremes of abiotic gradients.

The main driver of increased realized trait variability of clades in particular sections of abiotic gradients may be the increased phenotypic response of their constituent species to variations in the abiotic conditions themselves (i.e. in soil, climate and the corresponding species compositions). But the main driver may also be the phenotypic response to other factors that increase in intensity or diversity at particular abiotic environmental positions, such as stronger competition pressures or more diverse biotic interactions in abiotically

intermediate environments. At the same abiotic position, different species of a clade may develop different phenotypic responses to these biotic factors. In the first case, we should expect increased trait variability within a clade to correspond to increased correlation between trait attributes and abiotic positions of species in that clade. In the second case, we should expect increased trait variability to correspond to decreased correlation between trait attributes and the abiotic environment.

Testing our hypotheses on the role of the abiotic environment on the realized trait variability within clades of a given region requires: (i) accounting for multiple traits; (ii) estimating levels of trait variability in all clades of a major taxon within a given region; (iii) comparing levels of trait variability in clades distributed across intermediate to extreme conditions along multiple abiotic gradients; and (iv) comparing the relationships between environment and trait variabilities within clades to those across the species pool. It also requires an appropriate taxonomic level to be analyzed. In angiosperms, genera are known to occupy different abiotic environmental positions (e.g. Prinzing et al. 2001) and naturalists observe that some genera are much more variable in trait attributes than others (Jäger & Werner 2002). Monophyletic genera (while being to some degree an arbitrary level of classification) may thus be a usable unit to study the role of the abiotic environment on the observed trait variability within clades.

Data on traits and on abiotic distributions of Angiosperm species along multiple abiotic gradients have recently become available for the Central European flora (Klotz et al 2002; Ellenberg et al. 1992). These data permit to quantify the variability of multiple traits for hundreds of genera distributed along multiple abiotic gradients in a given region. Although these data are the best available, the fact that some of the genera originate from far outside this region and are represented by only few species in Central Europe may bias our results. Central Europe may represent only a small proportion of the global spectrum of abiotic

conditions covered by these genera. However, for many genera we know the percentage of the global species pool represented within Central Europe and can thus explore whether poorly represented genera bias the results. Moreover, except for temperature and continentality, abiotic gradients are well represented in Central Europe covering the entire global and historical range that can be encountered by genera (e.g. for moisture gradient, a soil cannot be moister than permanently submerged, and less moist than a south-facing rock or sand dune).

In this study, we aimed at quantifying the role of the abiotic environment on the realized variability of life-history traits within Central European plant genera. We first verified whether genera differ in their levels of trait variability. We also verified whether genera are an appropriate taxonomic level to study trait variability, by estimating the conservation level of traits across the Angiosperm taxonomy. We then asked: (i) Does trait variability depend on the age of genera? (ii) Does trait variability depend on the positions of genera along abiotic gradients? We tested observed patterns of within-genus variability for possible geographical sampling biases and phylogenetic biases. (iii) Are relationships between environment and trait variabilities within genera similar to those within the entire species pool? (iv) Does increased variability of a trait within a genus relate to an increased or to a decreased correlation of that trait to the abiotic environment within that genus?

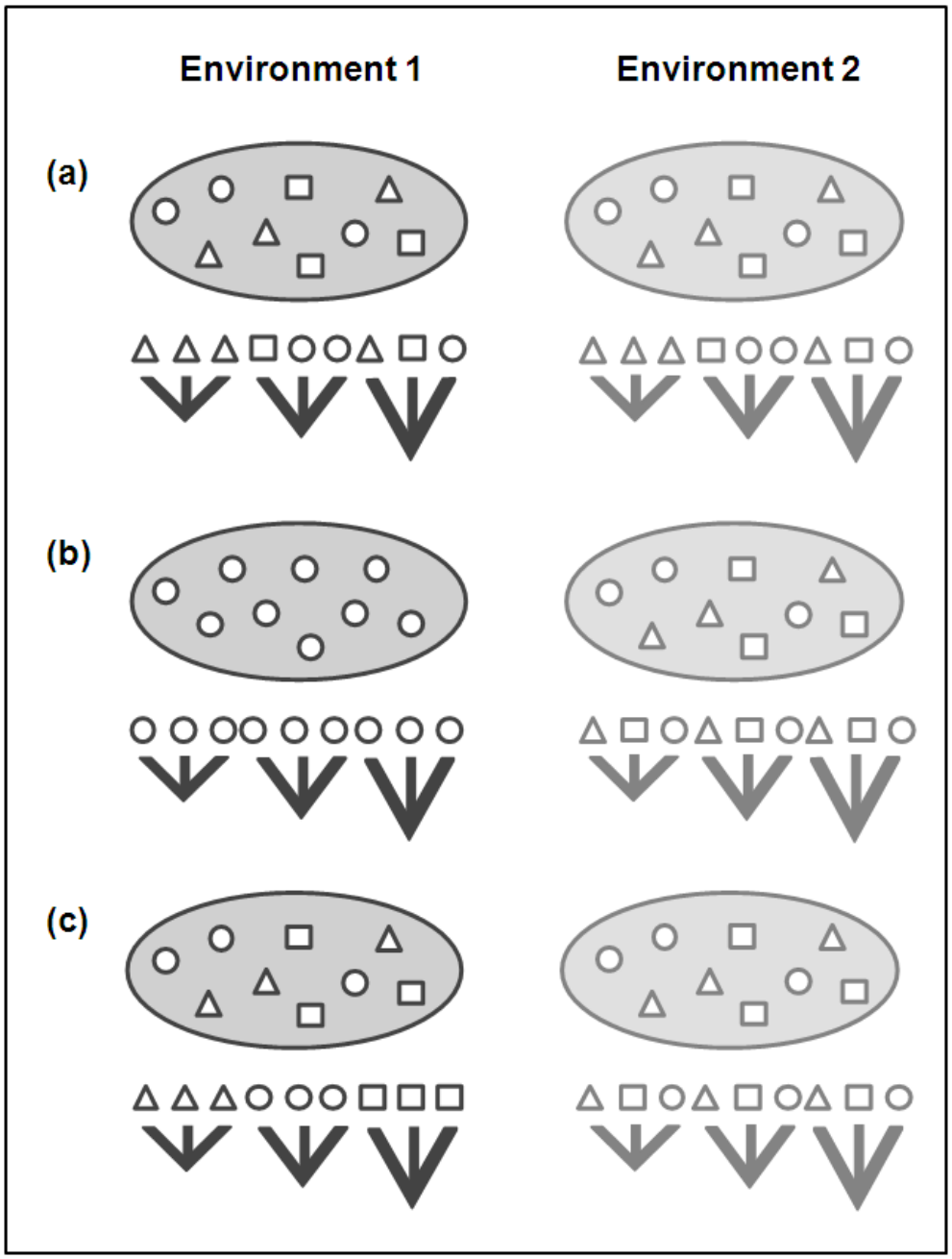

Figure III.1 Illustration of the different hypotheses explaining variation of trait variability realized within clades across a region. Ellipses in light and dark grey are two different environments characterized by specific environmental species pools. White circles, triangles and squares are different attributes of the same trait for nine different species. Species belong to either of six different clades (three species per clade). In hypothesis (a), realized trait variability within clades only depends on the age of the clades, older clades show larger variability. In hypotheses (b) and (c) realized trait variability within clades depends on the opportunities to establish and maintain diverse trait states in a given environment. In hypothesis (b), environmental opportunity operates across all species of the species pool and incumbent clades reflect the trait variability of their respective environmental species pools. In hypothesis (c), environmental opportunity is specific to species belonging to the same clade (for instance due to interaction with closely related competitors or with specialized pollinators or phytophages), and thus it affects only within-clade trait variability.

III. Materials and Methods

III.1. Databases

We extracted life-history traits from a database of the Central Europe flora, BiolFlor (Klotz *et al.* 2002). The species were classified into 838 genera and 131 families in the BiolFlor Database. Nomenclature and classification followed mainly Jäger & Werner (2002) and the Angiosperm Phylogeny Group III (Bremer *et al.* 2009). Sixty traits were available. We chose to work on life-history traits known to respond to environmental changes (Smith et al. 1997). We excluded traits that strongly varied within species (such as plant size), that were unavailable for many species (such as specific leaf area) or that were coded on a categorical scale (rendering calculation of trait variability difficult and incoherent with ordinal and continuous traits). We retained beginning of flowering, duration of flowering, plant life span, $\log_{10}$-seed mass, stress tolerance, and type of reproduction (as defined in Table III.1). These traits are classical life-history traits, except stress tolerance which is rather an indicator of the plant's ecological performance and depends on the coordinated responses of multiple life-history traits to environmental factors (Violle et al. 2007). Where there were multiple values for a species we took the mean. Multiple values per species were rare for most traits (0.03% to 6% of the species) except for seed mass (80% of the species). The multiple values of seed mass for a given species were mostly similar (mean coefficient of variance was 0.03).

The position of species along six abiotic gradients is given by Ellenberg indicator values: luminosity (L), temperature (T), continentality (C), moisture (M), soil reaction (R) and nitrogen content (N) (Ellenberg 1992). These positions ("Ellenberg indicator values") are estimates of the realized optimum habitat of each plant species and are expressed on ordinal scales of 9 to 12 ranks (see Table III.S1 in Supporting Information). It would be much better to have for all species measured values rather than expert-knowledge classifications such as those by Ellenberg. However, comparisons between Ellenberg values and direct

measurements of environmental gradients revealed strong correlations (Hill & Carey 1997; Diekmann 2003; Ozinga et al., 2004). These studies convincingly demonstrated the utility of Ellenberg values as environmental characteristics. It may be also better to construct habitat distribution models of species (Guisan & Zimmermann 2000). However, grained distributional informations are still missing for various Angiosperm genera at the scale of Europe. Moreover, these species distribution models can not yet account for major ecological parameters strongly contributing to species distribution, such as soil properties or resources requirements (Hanspach et al. 2009). Such ecological parameters allow a small-scale habitat description of species within a region (Guisan & Thuiller 2005). Ellenberg values for light, soil moisture, soil pH and soil nitrogen provide such information. We used the Ellenberg values for 2626 species, 757 genera and 126 families listed in the BiolFlor database. We calculated for each genus the mean position along each abiotic gradient. Note that the use of Ellenberg values as if they were continuous, e.g. calculating means on them, lead statistically to sound results (Ter Braak & Gremmen 1987).

4.3.2. Age of genera

We constructed a dated phylogeny based on data available for 554 genera (Appendix III.S1). Two measures of ages of genera were calculated: stem-node age and crown-node age (Appendix III.S1). Stem-node age means the age of the split of a genus from its sister clade. Crown-node age means age of the oldest split within a genus, more precisely – within the sample of a genus (e.g. the flora of the Central Europe). We related the ages of genera to their trait variability. We only present the results based on crown-node ages as they reflect time over which the contemporary species within a genus have diversified. Nevertheless, the use of stem or crown-node ages in the analyses led to very similar conclusions.

Table III.1 Definition of the six studied traits*.

Traits	Distribution	Definition
Flowering phenology (begin and duration)	Continuous	Flowering phenology refers to the start and the length of flowering period (given in months) that are typical for Germany.
Life span	Ordinal	The life span refers to the classes of life span and to the number of generative reproductions. 1: annual; 2: biennial; 3: pluriennial-hapaxanthic (species produces flowers and fruits only once and then dies); 4: pluriennial-pollakanthic (species may repeatedly produce flowers and fruits).
Seed mass	Continuous	Mean mass of diaspores and germinules (mg, $\log_{10}$-tranformed). Note that this was measured excluding structures that do not contribute to the development of the seed and is hence equivalent to the standard protocol applied by many authors for measuring seed mass (Cornelissen *et al.* 2003).
Stress tolerance	Ordinal	Stress tolerance follows the system of Grime (1977). 0: competitors, competitors/ruderals and ruderals; 0.5: competitors/stress-tolerators, stress-tolerators/ruderals and competitors/stress-tolerators/ruderals; 1: stress-tolerators.
Type of reproduction	Ordinal	1: sexually; 2: mostly sexually, rarely vegetatively; 3: sexually and vegetatively; 4: mostly vegetatively, rarely sexually; 5: vegetatively.

* Klotz S, Kühn I, Durka W (2002). *BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.

III.3. Trait variability within genera

We first ensured that species-within-genera is overall an appropriate taxonomic level for characterizing the variability of the life history traits selected. (Appendix III.S2). We then calculated the observed trait variability within a genus as the standard deviation of attributes of a given trait across species within the genus. We found that even standard deviations suffered from sample size bias: genera with a very small number of species showed lower standard deviations than larger genera even after randomizing species across genera. We thus corrected the observed standard deviations for a null expectation for a given species richness as explained in Appendix III.S3. We excluded monotypic genera. We did not aim for a multivariate description of trait-variability (e.g. Petchey *et al.* 2004) as different traits may be unequally influenced by ecological processes. In fact we found that different traits showed different relationships to abiotic factors and thus high variability in one trait would be hidden by low variability in another trait (see Results). We also characterized genera by their mean for each trait and for each abiotic gradient. Note that the use of Ellenberg values as if they were continuous, e.g. calculating averages on them, lead statistically to sound results (Ter Braak & Gremmen 1987).

A possible alternative to characterizing trait variability within genera is to quantify sister-lineage differences, i.e. absolute phylogenetically independent contrasts (Felsenstein 1985; Martin & Hansen 1997). We present analyses based on absolute phylogenetically independent contrasts in Appendix III.S4.

4.3.4. Trait variability realized within genera along abiotic gradients

Relationships between trait variability of genera and their positions along the six abiotic gradients were explored using a quadratic model (StatSoft 2010). The mean trait value across the species of a genus was integrated as a co-variable because standard deviations may be

related to means. In order to reduce multicollinearity among independent variables we conducted a best-subset search, using adjusted R^2 as a search criterion (i.e. the goal was not to identify a minimum set of predictor variables like we can do with Akaike or Mallow criteria, but to maximize the explained variance while accounting for the remaining degrees of freedom). In a second analysis we integrated the position of genera within families as a co-variable, as different families may differ in their capacity to shift traits (for instance families of herbaceous vs. tree life-form; Petit & Hampe 2006). Monotypic families were excluded. For two thirds of the genera, age was available. Inclusion of age into the regression model led to qualitatively the same conclusions: six significant relationships remained (all hump-shaped), two were lost (one hump-shaped and one hollow-shaped) and three were gained (one-hump-shaped and two hollow-shaped). However, inclusion of age reduced sample size considerably and so we only present the results without age as a co-variable. The distribution of residuals of each regression approached homogeneity and normality. We had to exclude one outlier (genus *Helleborus*) for "beginning of flowering" to ensure residuals approaching homogeneity and normality. This exclusion did not change the results. We illustrated the strongest and the weakest significant relationships between trait variability and abiotic gradients using plots of partial residuals. We finally explored the effect of geographical sampling on the observed relationships (Appendix III.S5).

III.5. Trait variability realized within the species pool along abiotic gradients

The observed relationships between environment and trait variabilities realized within the approximately 300 genera might reflect the relationship between environment and trait variability realized across the entire species pool (i.e. independent of the position of species in genera, Fig. III.1c). To explore this possibility, we randomly sorted the species into 300 groups of equal size, calculated environmental positions and trait variabilities for each of

these random groups and analyzed relationships between environment and trait variabilities as explained above (obviously, without family as a co-variable). We verified whether relationships observed across real genera re-appear across these 300 random groups, i.e. reflect relationships realized in the underlying species pool.

III.6. Relationship between variabilities of a trait within genera and the correlation of this trait to abiotic gradients

We first described the degree to which species within genera follow the general relationship between environment and trait attributes across all species. We tested across all species the relationship between attributes of a given trait and species Ellenberg indicator values. We used a linear model as quadratic relationships were very rare and increased explained variance very little (ranging between 1% and 2%, once 4%). As in the above regression analyses the position of species within families was integrated as a co-variable because many of the traits were conserved at the family level (Appendix III.S2) and models without family as a co-variable had a poor distribution of residuals. As above, monotypic families were excluded. The distribution of residuals approached homogeneity and normality. The absolute residuals from these regression models indicated to what degree a given species followed the general relationship between abiotic environment and a given trait. We found that genera differed significantly in the absolute residuals of their constituent species (6 traits, n = 456 – 1514 species, ANOVA, $F = 1.41 – 3.54$, $P < 0.001$). We then averaged, for each trait analyzed, absolute residuals within genera. Genera that have high scores are those whose constituent species poorly followed the general relationship between environment and attributes of a given trait.

We tested whether genera whose constituent species follow well the general relationship between abiotic environment and trait attributes are those that show particularly high or

particularly low trait variability. For this purpose we correlated, for a given trait, the above mean absolute residuals within genera to their respective trait variabilities. A positive relationship would indicate that genera whose constituent species follow well the general environment/trait relationship show particularly low trait variability.

IV. Results

IV.1. Trait variability differed between genera

For the six traits studied, the degree of trait variability highly significantly differed between genera (n = 774 – 2253 species, Levene test, F = 2.08 – 11.96, P < 0.001). This indicates that trait attributes are highly variable in some genera but relatively uniform in others (Fig. III.2 for an example). Trait variabilities of genera were almost independent of their species richness (n = 173 – 368 genera, linear correlations: R^2 < 0.03, mean 0.0088, quadratic correlations: R^2 < 0.08, mean 0.03; see also Appendix III.S3).

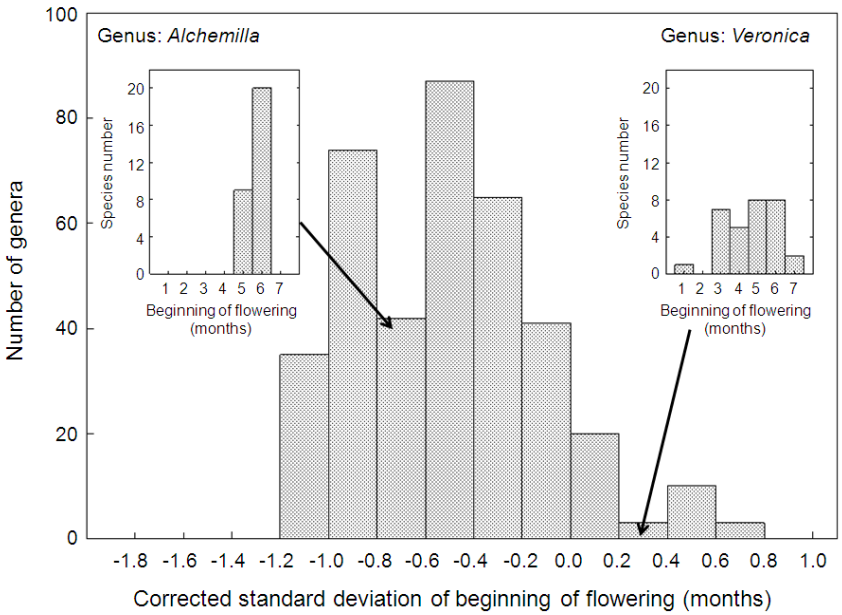

Figure III.2 Distribution of within-genus variabilities of the trait "beginning of flowering". For each genus, variability was quantified as the standard deviation corrected for a null expectation (Methods). Examples: genus *Alchemilla* (n = 29 species; corrected standard deviation = -0.69, i.e. variability lower than expected by random) and genus *Veronica* (n = 31; corrected standard deviation = 0.26, i.e. variability greater than expected by random).

IV.2. Trait variability did not depend on age of genera

Correlations between the crown-node ages of genera and their trait variabilities are not significant (n = 145 – 340 genera, linear correlations: $R^2 < 0.003$; $P > 0.26$, quadratic correlations: $R^2 < 0.03$, $P > 0.11$). Older genera do not have higher trait variability.

IV.3. Trait variability within genera is higher under intermediate abiotic conditions

The quadratic models without position of genera within families as a co-variable are highly significant for all studied traits (n = 173 - 368; $R^2 = 0.06 - 0.25$; $P < 0.001$) (Table III.2). We found seven significant quadratic hump-shaped relationships between trait variability and abiotic variables (Fig. III.3), i.e. the significant linear terms of abiotic variables (i.e. L, T, C, M, R and N in Table III.2) were positive and the significant quadratic terms of the same abiotic variables (i.e. L^2, T^2, C^2, M^2, R^2 and N^2 in Table III.2) were negative. This hump-shaped pattern was found for five of the six studied traits (i.e. all except life span). Note that the maxima of the hump-shaped functions were within the abiotic range included into analyses (examples in Fig. III.3). These results indicate that, overall, trait variability within genera is higher in the middle of abiotic gradients. Two significant quadratic relationships were lost (both hump-shaped) and two were gained (one hump-shaped and one hollow-shaped) after inclusion of family as a co-variable (Table III.2). Nevertheless, the same conclusions remained.

We also explored the effect of geographical sampling on the observed relationships and we found none (Appendix III.S5). The absolute residuals from our multiple quadratic regression models were not correlated to the representation of genera within Central Europe. Moreover, genera of high trait variability in Central Europe also seem to show high trait variability in a distant geographic region (at least for one trait, see Appendix III.S5).

Table III.2 Change of trait variability along abiotic gradients: results of multiple quadratic regression models of trait variability within genera (corrected standard deviations of traits) against positions of genera along abiotic gradients (mean Ellenberg indicator values). Analyses without (-) and with (+) position of genera within families as a co-variable. Variable selection by best-subset selection. The table gives β values for the predictive abiotic variables (L: light; T: temperature; C: continentality; M: moisture; R: reaction; N: nitrogen) and for the co-variable Trait-mean, F values for the co-variable Family, degrees of freedom (df) and determination coefficients (R^2). $^{\#}$ P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

	Co-variable Family	L	L^2	T	T^2	C	C^2	M	M^2	R	R^2	N	N^2	Trait-mean	Family	df	R^2
Begin of flowering	-	1.04*	-0.89*		-0.15**	-0.06		0.37	-0.39					-0.21***	-	352	0.10***
	+	0.71	-0.65		-0.14*									-0.14	0.09	272	0.25***
Duration of flowering	-			0.48$^{\#}$	-0.42		-0.05	0.64**	-0.66**		0.10		-0.15*	0.48***	-	352	0.25***
	+			0.63*	-0.63*			0.70*	-0.75*	-0.44	0.53$^{\#}$		-0.12$^{\#}$	0.41***	1.03	269	0.36***
Life span	-	0.11$^{\#}$		0.07			-0.07		-0.07			0.12*		-0.21***	-	354	0.12***
	+										0.08			-0.21***	2.35***	275	0.34***
Seed mass (log_{10})	-					-0.94$^{\#}$	1.04*	1.67***	-1.55***	-0.77$^{\#}$	0.49		-0.08	0.17*	-	159	0.23***
	+					-1.48**	1.58**	1.40**	-1.13*	-0.15			-0.17	0.25*	1.85*	113	0.45***
Stress tolerance	-	0.19***						0.97**	-1.01***			0.87**	-0.81**		-	342	0.09***
	+	0.19**			-0.09			1.13**	-1.04**	-0.48	0.54	0.90**	-0.94**		1.97***	265	0.30***
Type of reproduction	-		-0.10$^{\#}$					0.76**	-0.88***	0.62*	-0.61*	-0.44	0.42	0.15*	-	352	0.07***
	+							0.77*	-0.82*	0.45	-0.50			0.17*	1.24	272	0.21*

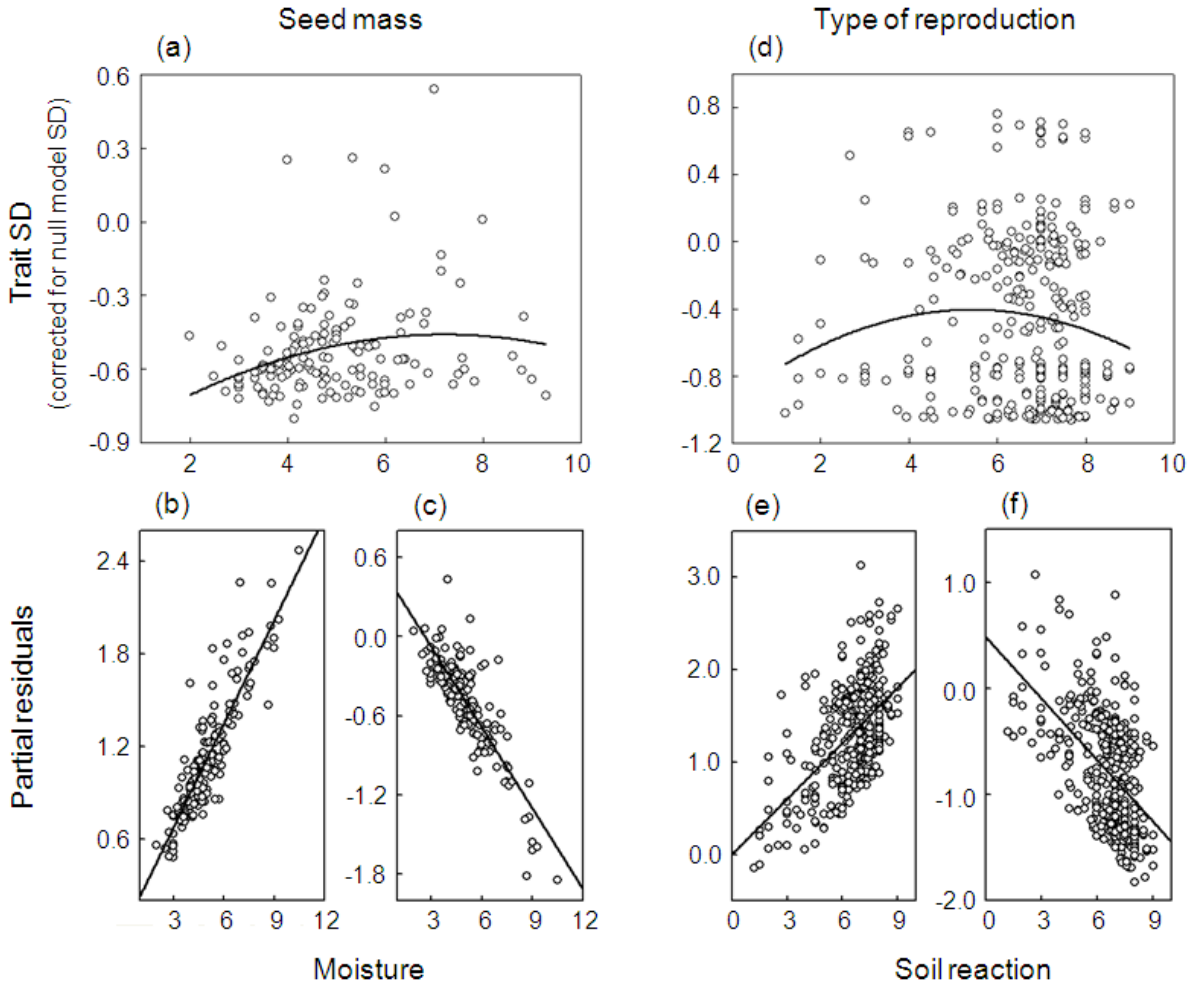

Figure III.3 Relationships between trait variabilities (corrected standard deviations, see Methods) and abiotic positions (Ellenberg indicator values) of genera: Plots of the strongest (i.e. seed mass against moisture) and the weakest significant relationships (i.e. type of reproduction against soil reaction). Figures a and d give the univariate relationships. Figures b, c, e, and f give the partial residuals from the multiple regression analyses in Table III.2 (without families as co-variable). Specifically, figures b and e give partial residuals for the corresponding linear terms, figures c and f those for the quadratic terms. These partial residual plots show the relationship between trait variability and a given abiotic variable while accounting simultaneously for the effect of the other independent variables included into in the model.

IV.4. Relationships between environment and trait variabilities within genera differ from those across the species pool

We found that out of the seven significant quadratic relationships observed between environment and trait variability within genera (explained above, Table III.2), only one was also found in the analysis across the 300 randomly assembled groups of species (hump-shaped relationship between moisture and the variability of type of reproduction, see Table III.3). In other words, only one significant relationship of within-genus variability reflected variation in the underlying species pool. All other significant relationships reflected genuine variation within-genera.

IV.5. High trait variability in genera showing little correlation of traits to abiotic gradients

The multiple linear regressions between traits of species and their positions along the six abiotic gradients are highly significant (Table III.S2). The absolute residuals from these regressions, averaged within genera, correlated positively to the trait variabilities of the same genera (for all traits except seed mass) (Fig. III.4). This indicates that the correlation between traits and abiotic gradients is weaker for genera of high trait variability.

The correlation between trait variability and mean absolute residuals might be a pseudocorrelation resulting from correlations between each of these two variables and the abiotic gradients. In this case, the variation explained by the former correlation should not exceed the variation explained by the two latter correlations taken together, i.e. the product of their respective explained variances. However, for each of the five significant correlations between trait variability and absolute residuals, we found that explained variances were much higher than what should be expected in case of a pseudocorrelation (R^2 = 0.08-0.2 vs. R^2*R^2 = 0.0002 – 0.01).

Table III.3 Results of multiple quadratic regression models of trait variability within 300 random groups (corrected standard deviations of traits) against positions along abiotic gradients (mean Ellenberg indicator values). Variable selection by best-subset selection. The table gives β values for the predictive abiotic variables (L: light; T: temperature; C: continentality; M: moisture; R: reaction; N: nitrogen) and for the co-variable Trait-mean, degrees of freedom (df) and determination coefficients (R^2). $^{\#}$ P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

	L	L^2	T	T^2	C	C^2	M	M^2	R	R^2	N	N^2	Trait-mean	df	R^2
Begin of flowering			-0.13*			-0.06	-1.39**	1.21*				0.14*	-0.15**	292	0.08***
Duration of flowering	-1.34	1.27				-0.07$^{\#}$		0.05				-0.06	0.65***	292	0.44***
Life span	-0.05		1.51***	-1.53***	-0.83**	0.86**	0.50$^{\#}$	-0.48$^{\#}$	0.65$^{\#}$	-0.65$^{\#}$	-0.37	0.31	-0.85***	286	0.74***
Seed mass (log_{10})		0.10		0.10									0.21**	233	0.06**
Stress tolerance	0.18**		-0.18**				-0.13*				0.84$^{\#}$	-0.67		293	0.07***
Type of reproduction			0.18**				1.43**	-1.41**					0.18**	294	0.07***

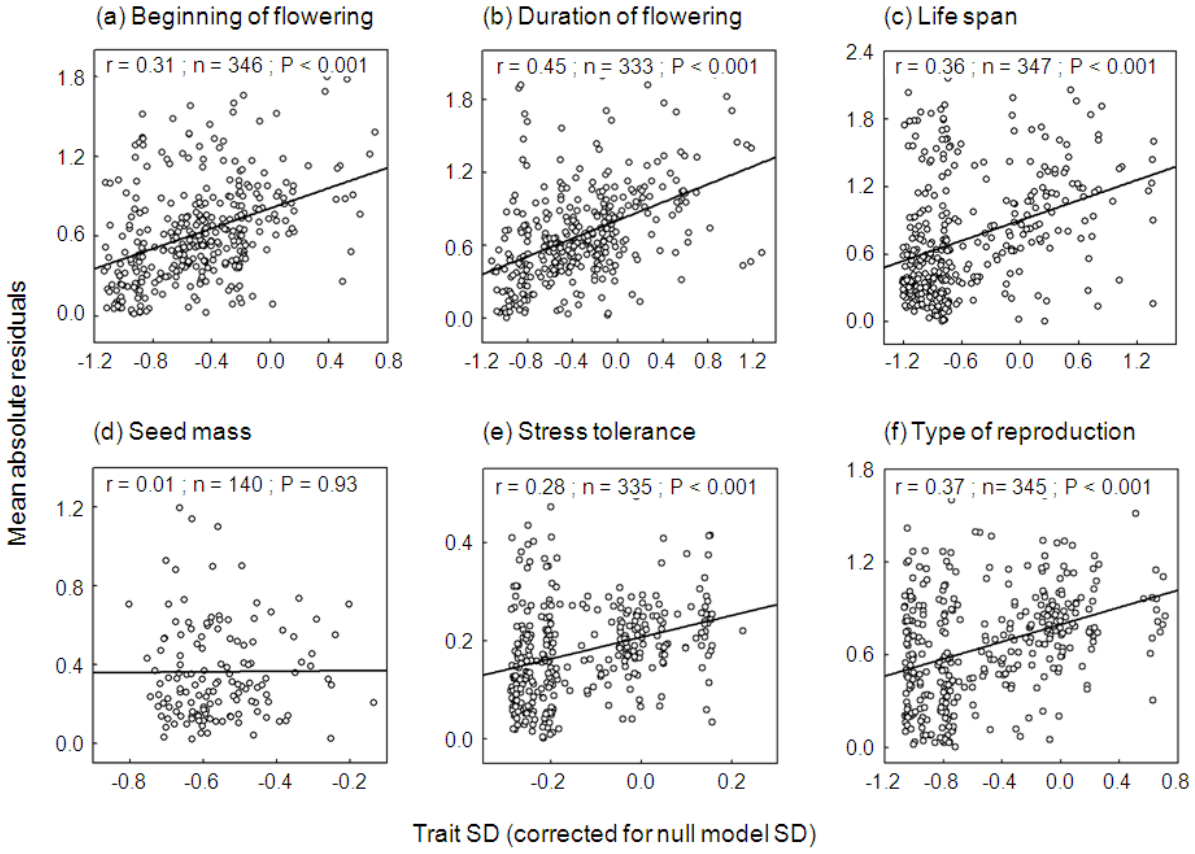

Figure III.4 Correlation between trait variabilities within genera (corrected standard deviations, see Methods) and the degree to which constituent species of genera follow the general relationships between abiotic environment and traits (mean absolute residuals from the multiple linear regressions of species traits against species Ellenberg indicator values). Traits are listed in Table III.1. Pearson correlation coefficient (r), sample size (n) and p-value (P) are given.

V. Discussion

This study aimed at explaining why within a given region some clades are highly variable in traits while others are not. We quantitatively confirmed that trait variability differs strongly among genera. This did not reflect the age of the genera, i.e. the time for trait diversification. It did, however, depend on the abiotic environment occupied. Trait variability within genera was higher in genera occupying intermediate position along abiotic environmental gradients. No such pattern was found across the regional species pool. This suggests genuine processes operating at the level of species within genera. Environmental opportunity for maintenance of diverse trait attributes seems specific to species belonging to the same genus, corresponding to scenario Fig. III.1c. Finally, increasing trait variability within genera reflected increasing independency of traits from the abiotic environment.

Although the data on the Central European flora were the best available, there are some potential issues in our data and methods. Some uncertainties remained about our regional approach based on a present-day pool of genera. First, analyses may be biased due to geographic sampling. However, we found that this is not the case (Appendix III.S4). Second, analyses might suffer from applying taxonomic categories, which albeit monophyletic, will be to some degree arbitrary. However, analyzing absolute phylogenetically independent contrasts (which suffered multiple other problems) showed that our general conclusions hold when avoiding taxonomy (Appendix III.S5).

One possible explanation for the increased trait variability under intermediate abiotic conditions is that here species may more easily survive physiologically outside the optimal abiotic environment. Each species may hence be exposed to a wider range of abiotic filters sorting a wide range of trait states (Crawford 2008). Ultimately, this may lead to the origin and persistence of high trait variability within clades occupying intermediate position along abiotic gradients (see also Liow 2007, Colles *et al.* 2009). This hypothesis implies that

increasing trait variability under intermediate abiotic conditions should result from particularly strong sorting by the abiotic gradients. However, we found that the increased trait variability rather reflects an increasing independence of the traits from the abiotic gradients.

Another perspective for explaining the increased trait variability in intermediate abiotic conditions is that extreme abiotic conditions may form narrow environmental filters that permit in each clade only the establishment of species with a particular traits attibute. For example, species within a clade growing under extremely acidic conditions may all share a particular trait state that confers tolerance to acidity (at the level of local communities: Helmus et al. 2007b). This explanation is not consistent with the hypothesis that increased trait diversification occurs at the extremes of ecological gradients due to a lack of competitors (Wilson 1959 cited in Crawford 2008; Ackerly 2003). This explanation, however, is consistent with our observations: increased match of traits to abiotic gradients in particular genera is correlated to decreased trait variability. Decreased trait variability in extreme abiotic environments may hence reflect environmental forcing of traits.

Environmental forcing in extreme abiotic environments assumes that the origin and maintenance of low trait variability reflects a strong direct effect of the abiotic environment itself (i.e. of the soil, the climate and the corresponding species compositions) on the species traits. It assumes that this direct effect is much weaker in intermediate abiotic environments. However, the main driver of high trait variability in intermediate abiotic environments might not be the direct effect of the abiotic environment itself, but rather other factors inherent to the intermediate abiotic positions of species. In particular, biotic interactions may be more important under intermediate abiotic conditions. In our study system, species richness is higher in the intermediate section of each gradient (Results not shown, see also Michalet et al. 2006; Bartish et al. 2010). Biotic filters and selection pressures, in particular competition, may be more powerful where the number of agents of filtering or selection, i.e. the number of

species, is higher (Grime 1987; Brooker & Callaway 1998). Competitive interactions may limit the coexistence of similar congeneric species (Lack 1943; Diamond 1975; Gotelli & McCabe 2002). Competitive interactions may be stronger in intermediate environments (Welden & Slauson, 1986), and the number of species per genus and thus of potential intrageneric competitors, is particularly high, too (Results not shown). Finally, the number of phytophages or pollinators specialized on particular plant clades might be highest in intermediate environments (for specialized interactions between phytophages and plant clades see Rezende et al. 2007 or Gossner et al 2009, for interaction strengths in intermediate environments see Oksanen et al. 1981). These powerful and diverse biotic filters and selection pressures in intermediate environments may thus permit the establishment of diverse traits attributes across species within a clade. We thus propose the hypothesis for future research that abiotically intermediate environments might increase the importance of biotic interactions for emergence and maintenance of high levels of trait variability within clades (see also Dodzhansky 1950; Fisher 1960; MacArthur 1969).

Our study indicates that intermediate abiotic conditions might play an important role in generating and maintaining trait variability in genera. This finding may have multiple implications. First, it suggests that the relationship between the number of genera in a community (or more generally its phylogenetic diversity) and the number of trait attributes in that community may be dependent on the abiotic context. In extreme abiotic environments phylogenetically aggregated communities consisting of only one or a few genera may be aggregated in their trait attributes, given that our results suggest that each of the constituent genera may vary little in trait attributes. In abiotically intermediate environments, however, even communities sampled from only one or few genera might show many trait attributes. This casts doubt on the widespread belief that phylogenetic diversity of communities can be

used as a simple proxy for the variability of trait attributes (Webb et al. 2002; but see Prinzing et al. 2008 or Swenson & Enquist 2009).

Secondly, increased variability of traits in intermediate environments may also have implications for conservation of functional variability under climatic or other anthropogenic changes. The impact of temperature increase (Feehan et al. 2008) and more frequent droughts and floods (Midgley & Thuiller 2007) on species diversity have been amply demonstrated. Moreover, humans also tend to render soil pH and soil nutrients increasingly extreme (Grieve 2001; Tilman 2002). Our findings indicate that these anthropogenic shifts towards more extreme abiotic conditions may also decrease the variability of functional traits realized within clades. This decreased trait variability may well trap entire clades. If particular trait attributes increase the extinction risk under human impact (Gaston & Blackburn 1996), and if entire clades share the same trait attribute, then extinctions in extreme environments will likely extinguish entire clades, i.e. entire branches of the tree of life (Mace et al. 2003).

Finally, our results suggest that anthropogenic shifts towards extreme conditions may not only decrease trait variability of plants, but also that of interacting species (e.g. pollinators, phytophages). Indeed, low trait variability in plants in particular abiotic environments may result in low trait variability in the interacting species (Johnson 2010). Reduced variability of flowering time, for instance, may result in reduced variability of phenologies of insect pollinators and phytophages, potentially affecting fundamental processes for plant species survival, which may have negative feed-back effects on the plants e.g. through paucity of particular pollinator species.

VI. Conclusion

Overall, we show that clades occurring in intermediate abiotic conditions have higher trait variability. This likely reflects environmental opportunities specific to clades, i.e. a

phylogenetically structured assembly of traits within a region. The main drivers of this high trait variability may not be the abiotic factors themselves, but rather stronger or more diverse biotic interactions under intermediate abiotic conditions. Intermediate conditions may play an important role in generating trait variability. Preservation of intermediate abiotic conditions, i.e. preventing anthropogenic shifts towards extreme conditions, may thus be an important challenge for the maintenance of functional versatility of entire plant clades and of the functional diversity of the ecosystems assembled from these clades. If consistent in time and across regions, the increased maintenance of trait variability within clades in intermediate environments should even result in an increased diversification of traits. We suggest testing this hypothesis in future research.

VII. Acknowledgments

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IX. Supporting information

Appendix III.S1 Method to estimate the age of genera.

Appendix III.S2 Variability of life-history traits explained across Angiosperm taxonomy.

Appendix III.S3 Method to correct trait variability within genera for species richness of genera.

Appendix III.S4 Quantifying trait variability using sister lineage differences.

Appendix III.S5 Effect of geographic sampling on the relationships between environment and trait variability.

Table III.S1 Definitions of the extremes of the abiotic environmental gradients.

Table III.S2 Change of species traits along abiotic environmental gradients.

Appendix III.S1 Method to estimate the age of genera.

To estimate ages of genera from the European angiosperm flora, we first reconstructed phylogenetic relationships in all angiosperm genera for which information was available. For each of the 554 genera, DNA sequences for at least one representative species were found in GenBank (http://www.ncbi.nlm.nih.gov). We searched GenBank for the five genes most commonly used in published phylogenetic studies of angiosperms from both chloroplast (*ndh*F, *mat*K, *rbc*L and *trn*L-*trn*F), and nuclear genomes (ITS1-5.8S-ITS2). To avoid large regions of missing data in our sequence matrices, we first created a matrix of rbcL sequences for 215 genera (*Amborella trichopoda* was included as outgroup), which was used to reconstruct phylogenetic relationships for all families in our sample and to estimate ages of splits between sister pairs of families. The sequences were selected so that each small family (less than five genera) was represented by all genera in the sample, and large families were represented by at least four genera each. Phylogenetic analyses within 24 large families (five genera and more) in our sample were performed separately for 21 sub-trees (in three cases two families were combined into a sub-tree), for which different sets of genes could be compiled from the Gene Bank (Table AIII.S1a).

We used Bayesian analysis (Rannala & Yang 1996; Yang & Rannala 1997) to estimate and search for phylogenies in all of our samples (the large sample of genera representing all families, the „family tree“, and the 21 sub-clades representing large families) by application of MrBayes 3.1.2 software (Ronquist & Huelsenbeck 2003). All data matrices were first tested against 56 models of DNA evolution in PAUP* 4.0 (Swofford 2002) and resulting scores were used to select models, which best fit the data. Our selection was based on the Akaike Information Criterion (AIC) (Akaike 1974) as implemented in ModelTest 3.7 (Posada & Crandall 1998). The results of these analyses were used to create input files for

MrBayes3.1.2, so that for each gene partition the closest model settings available in the program were specified. To allow estimation of substitution parameters for each region of DNA separately, we decoupled parameter estimation across the datasets. The Bayesian searches were based on $2.0*10^5$ to $4.0*10^6$ generations (Table AIII.S1a) with Markov chain Monte Carlo (MCMC) starting from random trees and vague priors (program‘s defaults). Trees were sampled every 100th or 1000th generation (depending on the total number of generations), providing from 2000 to 4000 trees in each of runs (for each data set at least two runs were used to confirm that they converged on similar stationary parameter estimates). The stationary (post burn-in) phase was determined in each analysis based on the average standard deviation of split frequencies (Huelsenbeck & Ronquist 2001) which are reported in Table AIII.S1a. The post burn-in trees were used to reconstruct a majority-rule consensus tree for each data set.

Divergence times among genera in a majority-rule consensus phylogram of the “family tree” (the tree with 215 representative genera of all families) were estimated using the Penalized Likelihood method (PL) of Sanderson (2002) using the software r8s version 1.70 (Sanderson 2004). We applied the Truncated Newton algorithm with bound constraints, which can handle age constraints and uses gradients for better convergence of rates. The outgroup taxon (*Amborella trichopoda*) was pruned prior to analysis. We used published age estimates for divergences at the base of the tree (Bremer 2000; Wikström et al. 2001; Bremer et al. 2004; Janssen & Bremer 2004; Moore et al. 2007) as fixed age constraints (Table AIII.S1b). Cross-validation was undertaken on the consensus tree to select an optimal smoothing value (Sanderson 2002). The analysis resulted in a chronogram with estimated ages of divergences among all families and among genera in small families.

As a next stage of our dating analyses, we reconstructed dated phylograms (chronograms) for all 24 large families in our sample, represented in the 21 sub-clades. The majority-rule consensus trees resulting from each of the Bayesian analyses (Table AIII.S1a) were further used in PL dating analyses, as described above. We used age estimates from our dating analyses on the "family tree" to provide the stem-node age for each of the 21 tree as fixed age constraint in PL analyses. The analyses resulted in chronograms, from which both stem and crown-node age estimates for all genera could be retrieved.

Table AIII.S1a Statistical results of Bayesian phylogenetic reconstructions of the "family tree" and within the largest families of angiosperms from the data set of Central European flora. Under N are numbers of clades. Numbers of terminal taxa include outgroups. In all analyses of the clades nuclear genome was represented by ITS sequences.

N	Family	Likelihood	STDev	PSRF	N taxa.	N gen.	cpDNA loci
1	Asteraceae	12093.0	0.014	1.008	55	$4.00*10^6$	rbcL
2	Apiaceae	9137.3	0.009	1.001	31	$1.25*10^6$	rbcL
3	Boraginaceae	6941.5	0.009	1.000	10	$1.00*10^6$	rbcL, trnL-trnF, atpß
4	Brassicaceae	20477.9	0.013	1.002	39	$1.00*10^6$	ndhF, matK
5	Campanulaceae	5636.4	0.007	1.000	7	$1.00*10^6$	rbcL, ndhF
6	Caryophyllaceae / Chenopodiaceae	16383.4	0.019	1.000	36	$3.00*10^6$	rbcL, matK
7	Cyperaceae	6913.6	0.009	1.000	14	$1.25*10^6$	rbcL, trnL-trnF
8	Dipsacaceae	12105.5	0.001	1.002	13	$1.00*10^6$	rbcL, ndhF
9	Ericaceae / Primulaceae	25438.8	0.002	1.000	19	$5.00*10^5$	rbcL, ndhF, matK
10	Fabaceae	15693.2	0.008	1.000	24	$1.25*10^6$	rbcL, matK
11	Gentianaceae	6390.9	0.004	1.000	7	$2.00*10^5$	rbcL, matK
12	Lamiaceae / Scrophulariaceae	13847.8	0.010	1.002	46	$2.50*10^6$	rbcL, trnL-trnF
13	Liliaceae	13961.9	0.006	1.000	20	$1.00*10^6$	rbcL, matK
14	Malvaceae	4707.4	0.001	1.000	5	$1.00*10^6$	rbcL, ndhF
15	Orchidaceae	12823.9	0.004	1.000	18	$1.00*10^6$	rbcL, matK, rpl16
16	Papaveraceae	7065.9	0.016	1.000	8	$1.25*10^6$	rbcL, trnL-trnF, rps16
17	Poaceae	20793.7	0.016	1.000	62	$1.50*10^6$	rbcL, matK
18	Ranunculaceae	14260.3	0.005	1.007	17	$1.00*10^6$	rbcL, matK, trnL-trnF
19	Rosaceae	13481.3	0.019	1.001	22	$1.00*10^6$	rbcL, matK
20	Saxifragaceae	7259.1	0.001	1.000	7	$5.00*10^5$	rbcL, matK
21	Solanaceae	8436.1	0.006	1.000	7	$1.00*10^6$	rbcL, matK, ndhF
	All-families tree	39995.6	0.018	1.003	215	$1.50*10^6$	rbcL

Table AIII.S1b Node age estimates from earlier studies used for calibration of the "family tree" of angiosperms from Central Europe. Under N are numbers of nodes.

N	Taxon	Node	Age	Reference
Fixed ages:				
1	Nymphaeales	stem	164	Moor *et al.* 2007
2	Mesangiosperms	crown	144	Moor *et al.* 2007
Monocots:				
3	Acoraceae	stem	134	Bremer 2000
4	Alismatales	crown	128	Janssen and Bremer 2004
5	Core_Monocots	crown	126	Janssen and Bremer 2004
6	Orchidaceae	stem	119	Janssen and Bremer 2004
7	Araceae	crown	117	Janssen and Bremer 2004
8	Poales	stem	117	Janssen and Bremer 2004
9	Butomaceae	stem	88	Janssen and Bremer 2004
10	Cyperaceae	stem	88	Janssen and Bremer 2004
11	Zosteraceae	stem	47	Janssen and Bremer 2004
Eudicots:				
12	Euasterids	crown	123	Bremer *et al.* 2004
13	Aquifoliales	stem	121	Bremer *et al.* 2004
14	Ericales	crown	114	Bremer *et al.* 2004
15	Apiales	stem	113	Bremer *et al.* 2004
16	Cornales	crown	112	Bremer *et al.* 2004
17	Asterales	stem	112	Bremer *et al.* 2004
18	Gentianales	stem	108	Bremer *et al.* 2004
Minimal ages:				
19	Malpighiales	stem	90	Moor *et al.* 2007
20	Fagales	stem	84	Wikström *et al.* 2001
21	Fabales	stem	60	Moor *et al.* 2007

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Appendix III.S2 Variability of life-history traits explained across Angiosperm taxonomy

We verified whether the level of species within genera is an appropriate taxonomic level for capturing a distinct portion of overall trait variability. To do so, we applied a variance components analysis (method of restricted maximum likelihood; StatSoft 2010) in order to estimate at which level of Angiosperm taxonomy species trait attributes are determined. Levels of taxonomic hierarchy were between-orders, between-families, between-genera and species-within-genera (Smith et al. 2006; Bremer et al. 2009). This method has proven to be robust and to give similar results as methods using phylogenetic information (Prinzing et al. 2001). A maximum variance in a trait at the level of species-within-genera, for instance, indicates that the trait varies most strongly within genera.

The variance components analysis showed a maximum of variance in species trait-attributes explained at the level of species-within-genera for all of the studied traits, except for seed mass (Table AIII.S2). The maximum of variance in seed mass was found at the level of genera within families (38.5 %), but even for this trait, a relevant part was explained at the level of species within genera (15.0 %). Overall, the genus level seems to be an appropriate taxonomic level for estimating trait variability within clades.

Table AIII.S2 Variance components analysis of trait attributes of species across angiosperm taxonomy. Data points are species, and percentage of variance explained at species level represents hence the variance unexplained by the analysis.

Variable	Percentage of variance explained			
	Species	Genus	Family	Order
Begin of flowering	41.2	21.8	21.7	15.3
Duration of flowering	65.5	23.9	0.5	10.1
Life span	43.3	39.0	14.1	3.6
Seed mass (log)	15.0	38.5	23.8	22.7
Stress tolerance	45.8	33.3	5.2	15.6
Type of reproduction	41.1	0.9	13.5	15.1
Mean	42.0	26.3	13.1	13.7

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Appendix III.S3 Method to correct trait variability within genera for species richness of genera

The observed variabilities within genera suffered from sample size bias: genera with a very small number of species showed lower variabilities than larger genera (even after randomized species across genera). We thus corrected the observed variabilities by calculating their difference from from the mean variabilities of a null model. The null model was created by reshuffling the species across genera 500 times (PopTools 3.1, www.cse.csiro.au/poptools/). This correction effectively suppressed any correlation to numbers of species per genus (Table AIII.S3a). Note that our aim was not to estimate significance of this difference between observed variabilities and null-mean variabilities. This would require additional division of the difference by the SD of the null model. However, as SD between samples (here: genera) increases when the size of the samples decreases, division by null-SD re-introduced a strong correlation to numbers of species per genus (Table AIII.S3a). We thus corrected our observed trait variability by only calculating the difference between observed variability and the mean of the corresponding null variabilities.

We verified whether the number of species within genera biased our core analyses, and whether this depends on how variabilities are corrected, i.e. whether or not the differences between observed and null-mean variabilities were divided by null-SD variabilities. For this we calculated our core analyses (Table III.2) with both ways of correcting trait variabilities and took the residuals. We found that residuals from analyses based on variabilities corrected with dividing by null-SD usually correlated strongly to species richness of the genera, contrary to residuals from analyses based on variabilities corrected without dividing by SD-null (Table AIII.S3b). Thus, the richness bias in the variabilities corrected with dividing by SD-null (Table AIII.S3a) results in a richness bias in the final analyses (Table AIII.S3b). We

finally included into these analyses the richness of genera as a co-variable. This indeed effectively made the richness bias in the residuals disappear. However, the results of these final unbiased analyses were now very similar to those of the analyses based on variabilities corrected without dividing by SD-null.

Table AIII.S3a Correlations between numbers of species per genus and trait variabilities corrected by (i) taking the difference between observation and mean of the null expectation, and (ii) taking the difference between observation and mean null expectation and dividing it by the standard deviation of the null expectation. Method (i) was applied in the rest of this study. Sample sizes (n), Pearson correlation coefficient (r) and p-values are given.

	n	Correction (i)		Correction (ii)	
		r	p	r	p
Begin of flowering	383	0.11	0.03	-0.27	<0.001
Duration of flowering	383	0.06	0.23	-0.08	0.12
Life span	383	-0.03	0.57	-0.59	<0.001
Log10 mean seed mass	172	-0.02	0.80	-0.51	<0.001
Stress tolerance	367	0.10	0.05	-0.28	<0.001
Type of reproduction	383	0.05	0.36	-0.56	<0.001

Table AIII.S3b Correlation between numbers of species per genus and the residuals of our core analyses (Table III.2), with these analyses being based on variabilities corrected by (i) taking the difference between observation and mean of the null expectation, and (ii) taking the difference between observation and mean null expectation and dividing it by the standard deviation of the null expectation. Method (i) was applied in the rest of this study. Sample sizes (n), Pearson correlation coefficient (r) and p-values are given.

	n	Correction (i)		Correction (ii)	
		r	p	r	p
Begin of flowering	383	0.10	0.05	-0.28	<0.001
Duration of flowering	383	0.04	0.40	-0.10	0.05
Life span	383	0.00	0.99	-0.56	<0.001
Log10 mean seed mass	172	0.00	0.99	-0.47	<0.001
Stress tolerance	367	0.05	0.32	-0.26	<0.001
Type of reproduction	383	0.02	0.69	-0.52	<0.001

Appendix III.S4 Quantifying trait variability using sister lineage differences.

A possible alternative to characterizing trait variability at the level of genera is to quantify sister- lineage differences, i.e. absolute phylogenetically independent contrasts (PICs, Felsenstein 1985; Martin & Hansen 1997) across the entire phylogeny. We also explored this option. We used a phylogenetic topology available from BiolFlor (Durka 2002). PICs were calculated for each trait, and for each abiotic gradient, using the CAIC software (Purvis & Rambaut 1995). We also recorded for each PIC the "values at nodes", characterizing the ancestor based on a weighted average across its descending sister lineages (Purvis & Rambaut 1995). We finally related for each trait the absolute PICs to the positions of the corresponding ancestors along environmental gradients using a quadratic model (as in the analysis across genera). We included the corresponding ancestral values of traits as covariables as trait divergence between descendents may be related to trait position of the ancestors.

We found that for each trait the means of the trait-PICs within genera correlated highly significantly to the trait variabilities calculated for the same genera (linear correlation: $R = 0.43 – 0.56$; $P < 0.001$), except for seed mass, the trait that varies least within most pairs of sister lineages. The relationships between absolute trait-PICs and environmental positions did not lead to precisely the same results as our approach based on trait-variabilities within genera (which is not surprising given the very different evolutionary amplitudes covered), but led nevertheless to qualitatively similar conclusions (Table AIII.S4): two significant quadratic relationships remained (both hump-shaped), six were lost (five hump-shaped and one hollow-shaped) and five were gained (four hump-shaped and one hollow-shaped). However, analyses of sister-lineage differences suffered from major non-normality and variance heterogeneity of residuals, independent of the transformation or standardization approaches applied. Analyses of trait

variability within genera did not suffer from these problems and we hence stuck to these analyses.

References

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Purvis A, Rambaut A (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences*, 11: 247-251.

Table AIII.S4 Results of multiple quadratic regression models of the difference in absolute PICs against ancestral positions along abiotic gradients. Variable selection by best-subset selection. The table gives β values for the predictive abiotic variables (L: light; T: temperature; C: continentality; M: moisture; R: reaction; N: nitrogen) and for the co-variable Trait-mean at nodes, degrees of freedom (df) and determination coefficients (R^2). # P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

	L	L²	T	T²	C	C²	M	M²	R	R²	N	N²	Trait-mean at nodes	df	R²
Begin of flowering	-0.36#	0.38#		-0.11***		-0.03	0.23	-0.25#	0.04		-0.19	0.21	0.19***	1283	0.05***
Duration of flowering	-0.05#								-0.32*	0.32*	-0.04		0.41***	1289	0.16***
Life span	0.07**		0.50***	-0.47**		-0.06*	0.22	-0.25#	0.10***				0.34***	1291	0.15***
Seed mass (log_{10})			0.08#					0.17***	0.84**	-0.94***		-0.15**	0.11*	469	0.07***
Stress tolerance	0.10***			-0.05			0.28	-0.34#		-0.05	0.81***	-0.72***	0.04	1218	0.04***
Type of reproduction	0.44*	-0.43*	0.30#	-0.28#			0.30*	-0.39**	0.07*				0.18*	1291	0.03***

Appendix III.S5 Effect of geographic sampling on the relationships between environment and trait variability.

In order to explore the effect of geographic sampling on the relationship between environment and trait variability, we first calculated the percentage of the global species pool represented in Central Europe for each genus. Data on global richness were available for 187 genera (from Angiosperm Phylogeny Group III, Bremer et al. 2009). Genera that were relatively well represented in Central Europe should suffer less from bias due to geographic sampling than poorly represented genera. Then, we correlated representativeness of genera to the absolute residuals from the multiple quadratic regression models in Table III.2 (with and without family as a co-variable). Absence of significant correlations would indicate absence of incidence of geographic sampling on the results. Negative correlations would indicate that the regression model is most appropriate for the geographically best represented genera, i.e. those for which the risk of geographic sampling bias is smallest. A positive correlation, however, would indicate that the regression model strongly reflects genera which suffer from geographic sampling bias and thus the results of the model themselves might suffer from such a bias. We found absolute residuals of genera from the regression models to be independent of representation of the same genera within Central Europe (for residuals from models without family as a co-variable n = 68 – 124 genera; Pearson r = 0.00 – 0.04, p = 0.65 – 0.99; for residuals from models with family as a co-variable: n = 65 – 117 genera; Pearson r = 0.02 – 0.15, p = 0.10 – 0.89).

As a second approach to verify a possible geographical sampling bias, we explored whether the trait variability of genera represented by Central European species is representative for the trait variability of the same genera in other regions. While for most traits no comparable comprehensive data bases exist for any other non-European region, the seed masses are known also for the flora of California (Jepson Flora Project, 2006. Ecological

Flora of California, 23 July 2006, (21 October 2009), http://ucjeps.berkeley.edu/efc/). We hence correlated within-genus standard deviations of seed masses represented by the Central European species against those represented by Californian species of the same genera. We used raw standard deviations for these comparisons, i.e. without correction by a null expectation (Methods), as this null expectation would differ between regions (however the conclusions are the same with and without correction). We found a significant correlation between the within-genus standard deviations of seed masses represented by the Central European species to those represented by Californian species of the same genera ($r = 0.39$; $n = 84$ genera; $p < 0.001$ or $r = 0.42$; $n = 90$; $p < 0.001$ with or without exclusion of six outliers, respectively), indicating that levels of within-genus variability for this trait do not depend on the geographic region of sampling.

References

Bremer B, Bremer K, Chase MW, Fay MF, Reveal JL, Bailey LH *et al.* (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, 161: 105–121.

Table III.S1 Definitions of the extremes of the environmental gradients*.

Environmental gradients	Extremes	Definitions
Luminosity (L)	1	Plants are in deep shade, may be less than 1%, seldom more than 30% full light irradiance intensity
	9	Plants are in full light, found mostly in full sun, rarely with less than 50% irradiance intensity
Temperature (T)	1	Plants are found only in high mountains (or in boreal-arctic regions), mostly in alpine and nival levels
	9	Plants grow in extremely warm conditions, spreading from the Mediterranean only into the warmest places of the upper Rhine valley
Continentality (C)	1	Plants grow in extremely seasonally constant temperature, only in few outposts in Central Europe
	9	Plants grow in extremely seasonally variable temperature, virtually absent from western central Europe
Soil moisture (M)	1	Extremely dry soils, e.g. bare rocks or sand
	12	Submerged plants, permanently or almost constantly under water
Soil reaction (R)	1	Plants grow in extreme acidity, never found on weakly acid or basic soils
	9	Lime indicators, always found on calcareous soils
Soil nitrogen (N)	1	Plants grow only in soils very poor in mineral nitrogen
	9	Plants are indicators of soils extremely rich in mineral nitrogen, such as cattle resting places, or near polluted rivers

* Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992). *Zeigwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica, Göttingen.

Table III.S2 Change of species traits along abiotic environmental gradients.

Results of the multiple linear regression models of species traits against species abiotic positions (Ellenberg indicator values). This table gives β values for the predictive abiotic variables (L: light; T: temperature; C: continentality; M: moisture; R: reaction; N: nitrogen), F values for the co-variable Family, degrees of freedom (df) and determination coefficients (R^2). $^{\#}$ P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

	L	T	C	M	R	N	Family	df	R^2
Begin of flowering	0.17***	-0.15***	0.04$^{\#}$	0.15***	0.02	0.05$^{\#}$	8.73***	1581	0.38***
Duration of flowering	0.07**	0.03	-0.06*	-0.04	-0.07**	0.13***	3.55***	1581	0.20***
Life span	-0.18***	-0.30***	0.07**	0.17***	0.15***	-0.21***	5.06***	1591	0.38***
Seed mass (log_{10})	-0.17***	-0.08*	-0.01	-0.19***	0.10**	0.14***	12.04***	471	0.59***
Stress tolerance	0.00	-0.20***	0.04$^{\#}$	0.18***	0.08***	-0.38***	4.26***	1491	0.37***
Type of reproduction	-0.18***	-0.15***	0.06**	0.27***	0.03	-0.10***	6.37***	1590	0.40***

Chapitre IV

Species coexistence and trait variability within genera: more partners, more traits?

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En préparation

Species co-existence and trait variability within genera: more partners, more traits?

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I. Abstract

The coexistence of plant species in local communities is often highly ephemeral. However, particular species might on average coexist with many species ("high-coexistence species") while others coexist only with few. Here we ask whether within a region (i) species in different evolutionary clades show different levels of coexistence, reflecting the characteristic environment, life strategy or the evolutionary age of the clades; (ii) clades composed of high-coexistence species establish increased variability of traits that mediate interactions among coexistent species. We studied species coexistence for 470 genera across 350,000 vegetation plots in the Netherlands. We found that levels of coexistence were significantly conserved within genera, independent of their species richness. Genera of high co-existence species were found in dark, cold, dry, nutrient-poor and high soil pH conditions, were characterized by high competitiveness or high ruderalness, and by a low phylogenetic age. Moreover, within-genus variability of 3 out of 5 traits was related to the level of coexistence of their constituent species. Highest trait variability was found either for genera composed of intermediate-coexistence species (life span, duration of flowering) or of low-coexistence species (seed mass). Overall, we conclude that the level of interspecific coexistence may be conserved within clades reflecting the conserved capacity to avoid replacement by competitors, ensure efficient colonization and use particular environmental extremes. Clades of high-coexistence species might maintain only little trait variability as they face increasingly diffuse competitive interactions which might induce convergence of trait states.

II. Introduction

Plant species coexistence and assemblage into communities are considered to be highly ephemeral, depending on variation in environmental requirements, disturbance or biotic interactions and arguably a lot of chance (Hubbell 2001; Amarasekare 2003; Shea et al. 2004; Silvertown 2004). While species coexistence has been extensively studied within local communities, it is less known whether across communities particular species tend to coexist on average with many species ("high-coexistence species") while others coexist only with few. It is not known whether the degree of species coexistence is ephemeral or conserved within clades. In other words, can we expect to find entire clades composed of high-coexistence species and clades composed of low coexistence species?

One reason why the degree of interspecific coexistence of plant species may be conserved within clades is that richness of locally coexisting species varies with the abiotic environment, and clades differ in the environments they use (niche conservatism – Webb et al 2002; Wiens & Graham 2005). Also, the size of the regional pool of potentially coexisting species differs between abiotic environments and hence between clades. Disturbance is another important environmental factor affecting both the richness of locally coexisting species, and the size of the regional pool of potentially coexisting species (Shea et al 2004). Again, different clades show different levels of disturbances, corresponding to different numbers of locally coexisting species. Finally, within the same environment, species of some clades may be much better equipped to displace competitors than species of other clades (competitive effect, Goldberg & Barton 1992). Species of these clades will thus coexist only with few other species. Alternatively, strong competitiveness may avoid displacement and hence successful coexistence with many species (competitive response, Goldberg & Barton 1992). Both abiotic environment and ecological strategy (i.e. competitiveness and disturbance tolerance) may vary with the age of clades (Field et al. 2004; Field & Arens 2005) and hence age of clades

may be a predictor of coexistence. We thus emit the hypothesis that the level of interspecific coexistence is phylogenetically conserved within clades, and that the level of coexistence of a clades' constituent species correlates to its abiotic environment, disturbance regime, competitiveness or age.

Differences in the levels of interspecific coexistence between plant clades may have multiple implications: in particular they may influence the observed trait variability within clades. Species coexistence may be mediated by traits, examples include the direct effect of competition on plant traits (Navas & Violle 2009) or the indirect effect via niches shifts on niche-related traits (Silvertown 2004), the trait response to natural enemies (Díaz et al. 2007), or to positive interactions with other species (e.g. facilitation, Gross et al. 2009). A high-coexistence species might hence succeed with either of many different trait states, and a clade of high-coexistence species might hence establish a large variability of trait states. In addition to such maintenance of high trait variability due to ecological processes of community assembly, traits may also diversify within clades in response to interactions with co-existing species, e.g. due to classical character displacement (Brooker et al. 2008; Pfennig 2009). In contrast, co-existence of a given plant species with only a single species, i.e. with itself in monoculture, may correspond to only a single optimal trait state, and to low trait variability in clades composed of such low-coexistence species. We thus emit the hypothesis that clades whose species locally coexist with many other plant species maintain (or even evolve) a larger variability of trait states than clades whose species coexist with only few other plant species.

Our above hypothesis that co-existence with many plant species increases trait variability within clades may apply only as long as coexistence leads to predictable pairwise interactions. However, with very large numbers of locally coexisting species the pairwise interactions between species may in fact become increasingly unpredictable and diffuse, resulting in maintenance of particular generalist trait states (Navarro et al. 2007). Within a given region

we might thus expect that clades maintain (or even evolve) the largest variability of trait states if their species locally coexist with an intermediate number of plant species.

Testing our hypotheses requires (i) estimating level of interspecific coexistence in all clades of a major taxon within a given region, (ii) comparing levels of interspecific coexistence in clades differing in age, in ecological strategy and in their distribution along multiple abiotic gradients, (iii) accounting for multiple traits and comparing levels of trait variability in clades differing in their level of interspecific coexistence. Data on plant species coexistence, multiple life-history traits and ecological strategy of Angiosperm species and on their distribution along multiple abiotic gradients have recently become available for the Netherlands (Schaminée et al. 1995-1999; Ellenberg et al. 1992; Klotz et al 2002). Testing our hypotheses also requires an appropriate taxonomic level to be analyzed. Angiosperm species belonging to different genera often tend to occupy different biotic and abiotic environments (Cavender-Bares et al. 2009, Prinzing et al. 2001) and naturalists observe since long that some genera are much more variable in trait attributes than others (e.g. Jäger & Werner 2002). Monophyletic genera (while being to some degree an arbitrary level of classification) may thus be a usable unit for such a macroecological study.

In this study, we asked: (i) Does the level of local interspecific coexistence differ between genera? (ii) Does the level of interspecific coexistence depend on the position of genera along abiotic gradients, on their ecological strategy and on their age? (iii) Does the level of interspecific coexistence of species affect the trait variability within a genus?

III. Material & methods

III.1. Species coexistence within genera

We extracted pairwise plant species coexistence data from the Dutch Vegetation Database (Schaminée et al. 1995–1999) containing spatially explicit descriptions of the species composition (presence ⁄ absence) in more than 350,000 small plots (plot sizes of several square meters, following standards in vegetation science, e.g. increasing with the size of the plants). We excluded trees (they are mostly planted and will not be much affected by the number of herb species growing below them), non vascular plant species (ferns, mosses, lichens, fungus, algae), as well as extremely rare, introduced species (their distribution is strongly human determined). The database provided for each species the proportion of plots where this species coexists with a particular plant species. The sum per species of these proportion gave the average number of locally pairwise coexisting species. We average these sums of proportion among the species of a genus to estimate the mean number of locally coexisting species of a species in this genus. We verified at which taxonomic level interspecific coexistence varied most strongly, by partitioning the variance in species coexistence between different levels of Angiosperm taxonomy (Appendix IV.S1).

III.2. Trait variability within genera

We extracted life-history traits from a database of the Central Europe flora, BiolFlor (Klotz et al. 2002), for 1080 species, 470 genera and 93 families in common with the SynBioSys database. Nomenclature and classification followed mainly Jäger & Werner (2002) and the Angiosperm Phylogeny Group III (Bremer et al. 2009). Sixty traits were available. We chose to work on life-history traits known to respond to environmental factors (Smith et al. 1997). We excluded traits that strongly varied within species (such as plant size), that were unavailable for many species (such as specific leaf area) or that were coded on a categorical

scale (rendering calculation of trait variability difficult and incoherent with continuous or ordered traits). We retained beginning of flowering, duration of flowering, plant life span, $\log_{10}$-seed mass and type of reproduction (as defined in Table IV.1). These traits are classical life-history traits (Violle et al. 2007). Where there were multiple values for a species we took the mean.

We first verified at which taxonomic level traits varied most strongly, by partitioning the variance in species traits at different levels of Angiosperm taxonomy (Appendix IV.S1). We then calculated the observed trait variability within a genus as the standard deviation of attributes of a given trait across species within the genus. We found that even standard deviations suffered from sample size bias: genera with a very small number of species showed lower standard deviations than larger genera even in the null model. We thus corrected the observed standard deviations to what we would expect by random given their species richness as explained in Appendix IV.S2. We excluded monotypic genera. We did not aim for a multivariate description of trait-variability (e.g. Petchey et al. 2004) as different traits may be unequally influenced by ecological factors. They showed different relationships to species coexistence levels and thus high variability in one trait would be hidden by low variability in another trait (see Results). We also characterized genera by their mean for each trait.

Table IV.1 Definition of the six studied traits*.

Traits	Distribution	Definition
Flowering phenology (begin and duration)	Continuous	Flowering phenology refers to the start and the length of flowering period (given in months) that are typical for Germany.
Life span	Ordinal	The life span refers to the classes of life span combined with the number of generative reproductions. 1: annual; 2: biennial; 3: pluriennial-hapaxanthic (species produces flowers and fruits only once and then dies); 4: pluriennial-pollakanthic (species may repeatedly produce flowers and fruits).
Seed mass	Continuous	Mean mass of diaspores and germinules (mg, log_{10}-tranformed). Note that this was measured excluding structures that do not contribute to the development of the seed and is hence equivalent to the standard protocol applied by many authors for measuring seed mass (Cornelissen *et al.* 2003).
Type of reproduction	Ordinal	1: sexually; 2: mostly sexually, rarely vegetatively; 3: sexually and vegetatively; 4: mostly vegetatively, rarely sexually; 5: vegetatively.
Competitiveness	Ordinal	Competitiveness follows the system of Grime (1977). 0: stress-tolerators, stress-tolerators/ruderals and ruderals; 0.5: competitors/stress-tolerators, competitors/ruderals and competitors/stress-tolerators/ruderals; 1: competitors.
Ruderalness	Ordinal	Ruderalnness follows the system of Grime (1977). 0: competitors, competitors/stress-tolerators and stress-tolerators; 0.5: competitors/ruderals, stress-tolerators/ruderals and competitors/stress-tolerators/ruderals; 1: ruderals.

* Klotz S, Kühn I, Durka W (2002). *BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.

III.3. Abiotic position of genera

The position of species along six abiotic gradients is given by Ellenberg indicator values: luminosity (L), temperature (T), continentality (C), moisture (M), soil reaction (R) and nitrogen content (N) (Ellenberg 1992). These positions ("Ellenberg indicator values") are estimates of the realized optimum habitat of each plant species and are expressed on ordinal scales of 9 to 12 ranks (see Table IV.S1 in Supporting Information). Comparisons between Ellenberg values and direct measurements of environmental gradients revealed strong correlations (Hill & Carey 1997; Diekmann 2003; Ozinga et al. 2004). These studies convincingly demonstrated the utility of Ellenberg values as environmental characteristics. We extracted the Ellenberg values for the 1080 species of our database. We characterized genera by their mean for each abiotic gradient. Note that the use of Ellenberg values as if they were continuous, e.g. calculating averages on them, lead statistically to sound results (Ter Braak & Gremmen 1987).

III.4. Ecological strategies of genera

We extracted the competitiveness and ruderalness (i.e. disturbance tolerance and colonization capacity) data for our 1080 species following the Grime's CSR ecological plant strategy scheme (Grime 1977). These data were available in the database BiolFlor (Klotz et al. 2002). In BiolFlor database, competitiveness and ruderalness were inferred from species characters, such as life form, leaf life span, leaf anatomy, maximal growth height, or pollination and dispersal modes. Although the CSR scheme has been criticized (Grace 1991), is has proven to be a good predictor of patterns of species coexistence in a given region (e.g. Carlyle et al. 2010). We ordered the competitiveness and ruderalness variables in three ranks, from 0 (non-competitive or non-ruderal species) to 1 (highly competitive or ruderal species), as explained in Table IV.1. We characterized genera by their mean for each ecological strategy variables.

III.5. Ages of genera

We constructed a dated phylogeny based on data available for 554 genera (Appendix IV.S3). Two measures of ages of genera were calculated: stem-node age and crown-node age (Appendix IV.S3). Stem-node age means the age of the split of a genus from its sister clade. Crown-node age means age of the oldest split within a genus, more precisely – within the sample of a genus (e.g. the flora of the Central Europe). We only present the results based on crown-node ages as they reflect time over which the contemporary species within a genus have diversified. Nevertheless, the use of stem or crown-node ages in the analyses led to very similar conclusions.

III.6. Statistical analyses

III.6.1. Interspecific coexistence within genera

We first compared mean numbers of locally coexisting species among genera using ANOVA (StatSoft 2010). We verified whether the observed pattern was increased with the species richness of genera or from the frequency of their constituent species in the plots (indicating a possible bias from rare, possibly undersampled species.).

III.6.2. Relationships between interspecific coexistence within genera and their abiotic position, competitiveness, ruderalness and age

We first tested the relationships between mean numbers of coexisting species of genera and their mean position along abiotic gradients, their mean competitiveness, their mean ruderalness and their age separately. We tested the relationships between mean interspecific coexistence of genera and their position along each of the abiotic gradients by univariate linear and quadratic regressions. We then tested the multivariate relationship between mean numbers of coexisting species of genera and their position along all of the six abiotic

gradients by a multiple linear and quadratic regressions. We tested the relationship between mean numbers of coexisting species of genera and their mean competitiveness by simple linear and quadratic regressions. We applied the same approach to test the relationship with mean ruderalness. Given the opposing effects that competitiveness or ruderality may have on coexistence (Introduction) we accounted for possible non-linearities by fitting a quadratic model. In a second analysis, we tested for the multivariate relationship between mean numbers of coexisting species of genera and both mean competitiveness and mean ruderalness, in order to account for interdependence of these two predictive variables. We then tested the relationship between mean numbers of coexisting species of genera and their age by a simple linear and quadratic regression. Finally, we tested the relationships between mean numbers of coexisting species of genera and their mean abiotic position, their competitiveness and ruderalness and their age by a multiple regression model, in order to account for the interdependence of all predictive variables. For this analysis, we conducted a best-subset search using Mallow criterion in order to reduce multicollinearity among independent variables and identify a minimum set of predictor variables. We verified whether each observed pattern depended on the species richness of genera by integrating species richness as a co-variable into the regressions. The distribution of residuals of each regression approached homogeneity and normality.

III.6.3. Relationships between mean interspecific coexistence and trait variability within genera

We tested the relationship between trait variability within genera and their mean numbers of coexisting species using multiple linear and quadratic regression models with a best-subset search using Mallow criterion. The mean trait value of a genus was integrated as a co-variable because variabilities may be related to means. We also integrated ages of genera as a co-

variable, as trait variability within genera may depend on their age (Ackerly & Nyffeler 2004). We did not account for the position of genera within families because this resulted in the exclusion the numerous genera that were the only representatives of their families and hence very strongly reduced the sample size (from 73 – 194 to 48 – 165 genera). In a second analysis, we included mean positions along the six abiotic variables as co-variables into the regression model, as environment was related to coexistence (see Results) and may also influence trait variability (e.g. Helmus et al. 2007a). The distribution of residuals of each regression approached homogeneity and normality. We had to exclude one outlier (genus *Vaccinium*) for "$\log_{10}$ seed mass" to ensure residuals approaching homogeneity and normality.

IV. Results

IV.1. Interspecific coexistence differs between genera

We found that genera significantly differed in their mean numbers of coexisting species (ANOVA, $n = 1080$; $F = 3.5$; $p < 0.001$). This indicates that interspecific coexistence of species was high in some genera but relatively low in others (Fig. IV.1 for an example). The mean numbers of coexisting species of genera was independent from their species richness (Pearson correlation, $n = 469$; $r = 0.01$; $p = 0.84$) and did not increase with the frequency of their constituent species in the plots (Pearson correlation, $n = 469$; $r = -0.11$; $p = 0.02$), i.e. there was no bias from rare, possibly undersampled species.

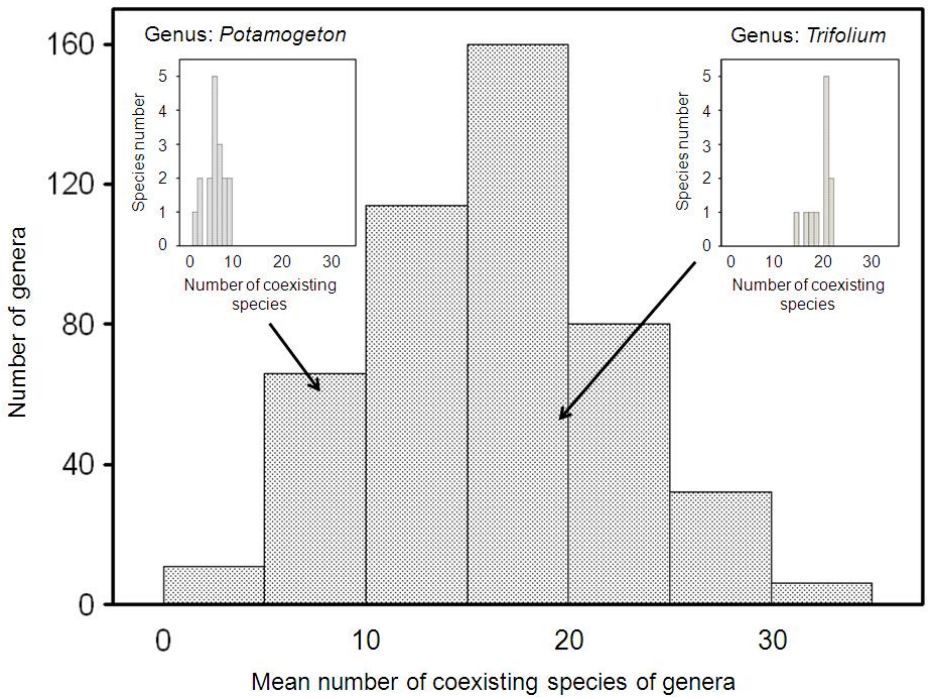

Figure IV.1 Distribution of the mean numbers of locally coexisting species within 470 genera. Examples: genus *Potamogeton* (n = 17 species; mean number of coexisting species = 550.0) and genus *Trifolium* (n = 11; mean number of coexisting species = 1972.2).

IV.2. Interspecific coexistence of genera depends on their abiotic positions, their competitiveness, their ruderalness and their age

The univariate relationships between mean numbers of coexisting species of genera and their mean positions along the abiotic gradient were linear, except for continentality and soil nutrient content. The coexistence level of genera linearly decreased with luminosity, soil moisture and linearly increased with soil pH. We found significant hump-shaped relationships with continentality and soil nutrient content. However, except for relationships with soil moisture (R^2 = 0.29), these univariate significant relationships were very weak (R^2 = 0.02 – 0.08), possibly due to interdependence of the abiotic variables. The multivariate model (R^2 = 0.46) yielded linear relationships: genera composed of high-coexistence species were found in dark, cold, dry, nutrient-poor and high soil pH conditions (Fig IV.2).

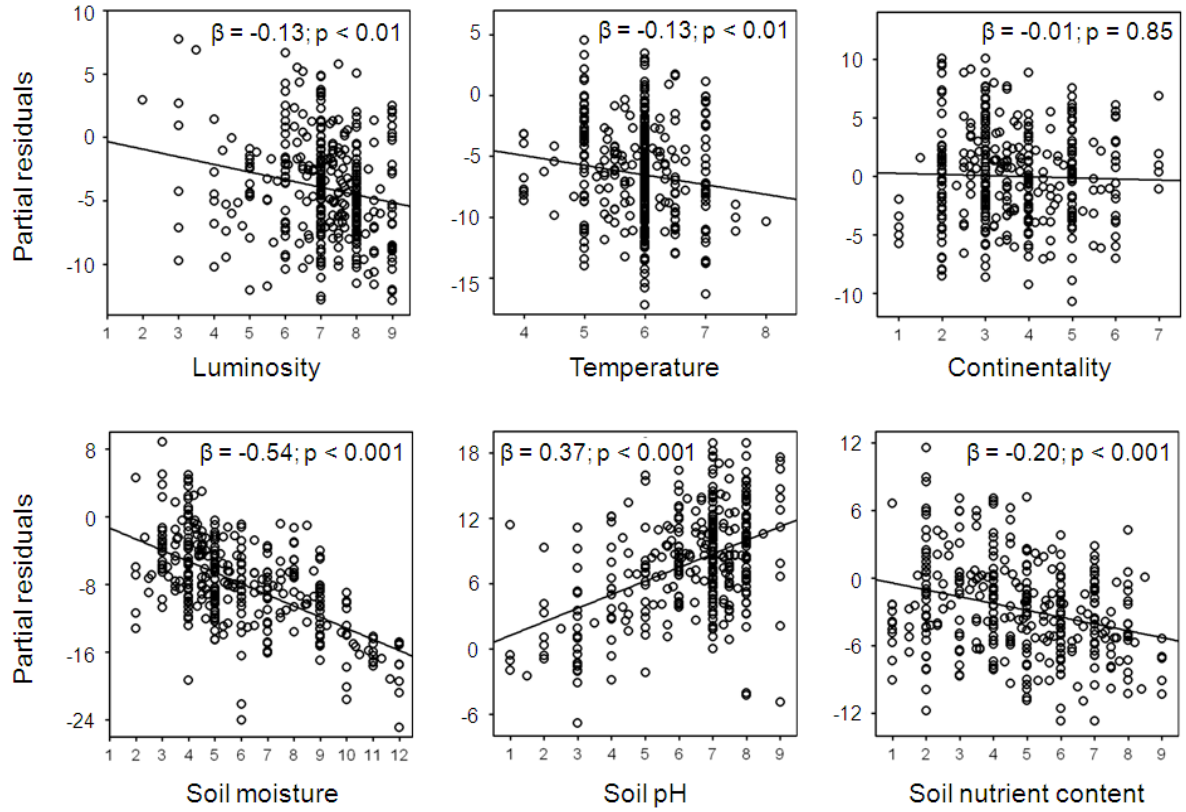

Figure IV.2 Partial residuals plots of relationships between mean numbers of coexisting species of genera and their mean positions along abiotic gradients (Ellenberg indicator values). These partial residual plots show the relationship between coexistence and a given abiotic variable while accounting simultaneously for the effect of the other independent variables included into in the model. Beta-values (β) and p-values (P) are given. R^2 of the entire model = 0.46.

The univariate regressions between mean numbers of coexisting species of genera and their mean competitiveness and ruderalness indicated significant hump-shaped relationships between these (Fig. IV.3a). However, when both predictive variables were included in the regression model, we found that mean interspecific coexistence linearly increased with mean competitiveness and ruderalness (Fig. IV.3b).

Finally, we found a linear relationship between mean numbers of coexisting species of genera and their age: interspecific coexistence significantly decreased with increasing age of genera (simple linear regression, n = 469; r = -0.16; p < 0.001).

Overall, the multiple regression between mean numbers of coexisting species of genera and their mean abiotic positions, competitiveness, ruderalness and age gave the same results

as when these groups of variables were tested separately (Table IV.2). All results were independent of the species richness of genera.

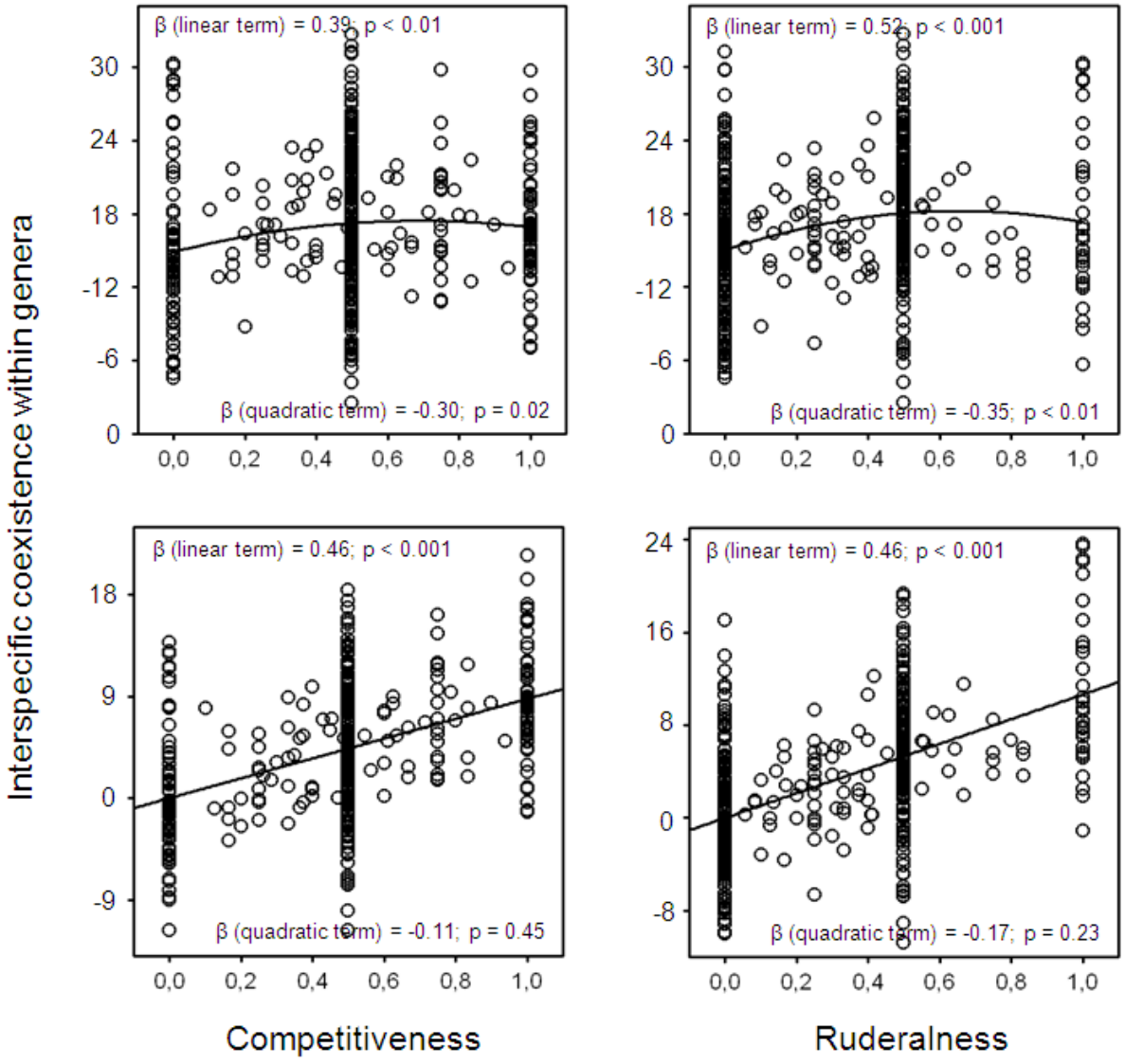

Figure IV.3 Relationship between mean numbers of coexisting species of genera and their ecological strategies. (a) and (b) give the univariate relationships between mean numbers of coexisting species of genera and their mean competitiveness and their mean ruderalness. (c) and (d) give partial residuals from multiple relationship between mean numbers of coexisting species of genera and both mean competitiveness and mean ruderalness. These partial residual plots show the relationship between coexistence and a given ecological strategy while accounting simultaneously for the effect of the other ecological strategy. Correlation coefficients (R), Beta-values (β) and p-values (P) are given.

Table IV.2 Results of multiple quadratic regression models of mean number of coexisting species of genera against their mean abiotic position (mean Ellenberg indicator values), mean competitiveness, mean ruderalness and age. Variable selection by best-subset selection. The table gives β values for the predictive variables and determination coefficients (R^2). n = 312 genera. ^{ns} P ≥ 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

	Mean number of coexisting species of genera
Luminosity	-0.14**
Temperature	-0.11*
Continentality	
Soil moisture	-0.34***
Soil nitrogen content	0.41***
Soil pH	-0.26***
Competitiveness	0.30*
Competitiveness²	-0.19^{ns}
Ruderalness	0.20**
Ruderalness²	
Age	-0.09*
R^2	0.42***

IV.3. Interspecific coexistence of genera is related to variability of some traits

The regression models without abiotic environment as a co-variable showed significant hump-shaped relationships between mean numbers of coexisting species of genera and their variabilities in duration of flowering and plant life span (Table IV.3a; Fig IV.4a, b). The significant hump-shaped relationship for life span remained after inclusion of the abiotic environment as co-variables (Table IV.3b; Fig. IV.4c) and a negative linear relationship was gained for $\log_{10}$ seed mass (Fig IV.4d). The significant hump-shaped relationship for duration of flowering was lost (Table IV.3b), but even when the abiotic variables were all excluded from this analysis, which indicates that the analysis failed in its function to sort out whether coexistence or coexistence-related environmental factors are more pertinent. For duiration of flowering, we hence maintain the result of the before analysis without environment as co-variables.

Table IV.3 Change of variabilities of five traits with mean numbers of coexisting species of genera: results of multiple quadratic regression models of trait variability within genera (corrected standard deviations of traits) against mean numbers of coexisting species of genera. Multiple models (a) without and (b) with mean abiotic positions of genera as co-variables. Variable selection by best-subset selection. The table gives β values for the predictive variable coexistence and for the co-variable age of genera and Trait-mean, degrees of freedom (df) and determination coefficients (R^2). ^{ns} P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

(a)	Begin of flowering	Duration of flowering	Life span	Log_{10}-seed mass	Type of reproduction
Mean numbers of coexisting species		0.73*	0.89**		0.07^{ns}
Mean numbers of coexisting species²		-0.70*	-0.83**		
Age	0.12^{ns}		-0.10^{ns}	0.20**	
Trait-mean	-0.19**	0.38***	0.23***	0.48***	
df	194	190	192	96	73
R^2	0.05**	0.19***	0.12***	0.28***	0.00^{ns}

(b)	Begin of flowering	Duration of flowering	Life span	Log_{10}-seed mass	Type of reproduction
Mean numbers of coexisting species			0.97**	-0.36**	
Mean numbers of coexisting species²			-0.91**		
Luminosity				-0.28**	
Temperature			0.20**		0.09^{ns}
Continentality					
Soil moisture				0.38**	
Soil nitrogen content				-0.40**	
Soil pH	0.13^{ns}				
Age	0.12^{ns}		-0.15^{ns}	0.20**	
Trait-mean	-0.25***	0.40***	0.23***	0.45***	
df	175	177	174	87	63
R^2	0.09***	0.16***	0.14***	0.39***	0.01^{ns}

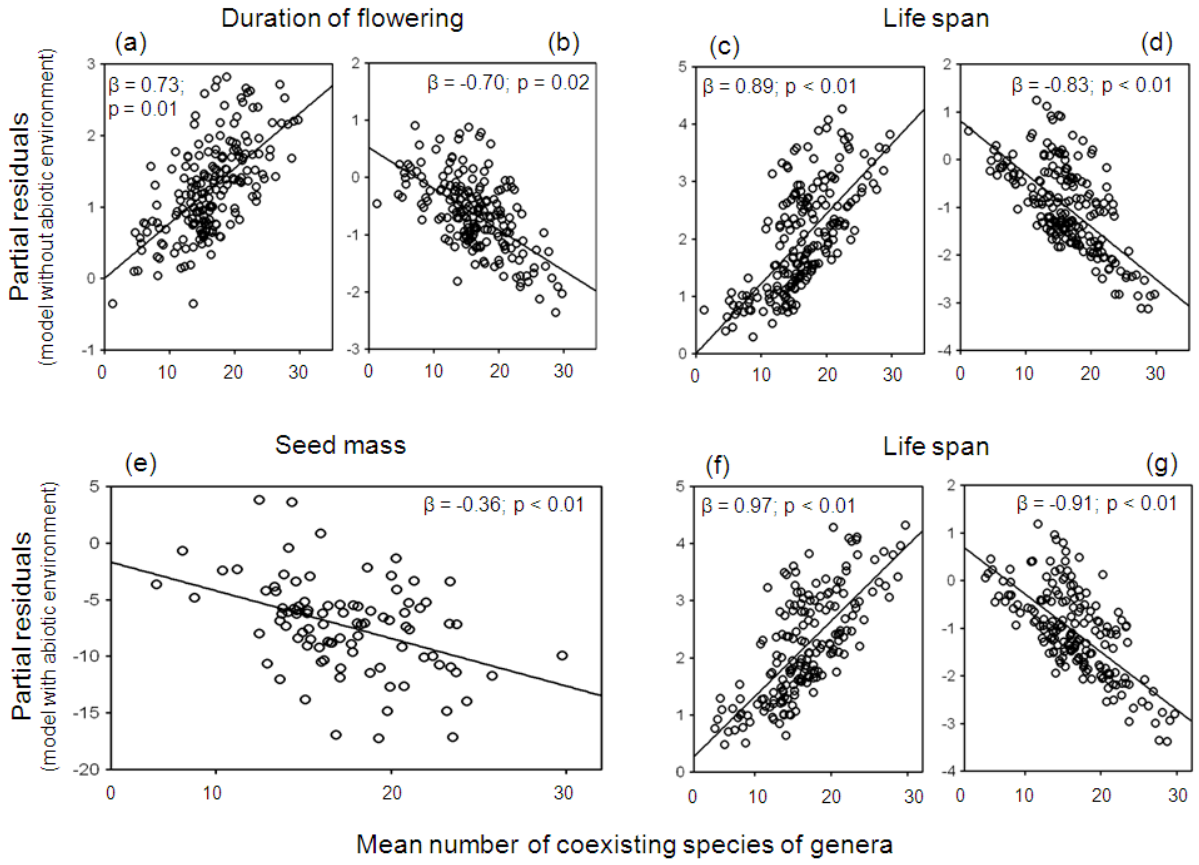

Figure IV.4 Significant relationships between trait variability and mean numbers of coexisting species of genera (see Table IV.3 for details on the no significant relationships). Figures a, b, c and d give the partial residuals from multiple regression analyses without abiotic environments as co-variables (Table IV.3a). Figures e, f and g give the partial residuals from multiple regression analyses with abiotic environments as co-variables (Table IV.3b). Figures a, c, e and f give partial residuals for the corresponding linear terms, figures b, d and g those for the quadratic terms. These partial residual plots show the relationship between trait variability and coexistence while accounting simultaneously for the effect of the other independent variables included into in the model. Beta-values (β) and p-values (P) are given.

V. Discussion

This study showed for the first time that genera differ in their mean number of coexisting species. We demonstrated that the level of interspecific coexistence of species within genera decreased with their environmental tolerance or preference to high luminosity, heat, soil moisture, soil nitrogen content and soil acidity. Coexistence linearly increased with competitive capacity and high disturbance tolerance when accounting for both variables simultaneously. In addition, we showed that the mean number of coexisting species of genera significantly decreased with increasing age of genera. Finally, we found that trait variability maintained within genera depended on the mean number of coexisting species for duration of flowering, life span and seed mass. The variability of the former two traits was highest for intermediate levels of coexistence and that of the latter for lowest levels of coexistence.

Although the data of species coexistence were the best available in the Netherlands flora, there are some potential issues in our data and methods. First, the mean number of coexisting species of genera might increase with their species richness and the frequency of their constituent species in the plots due to simple numerical sampling effects. However, we verified this was not the case. Second, we worked on instantaneous data of species coexistence. Thus, these data did not reflect the past species interactions, which may influence the present observed relationships within genera. Finally, measures of trait variability may be biased due to geographic sampling, i.e. due to the fact that some of the genera originate from far outside this region and are represented by only few species in The Netherlands. Both shortcomings, might introduce noise in our analysis, but it is not obvious in how they might introduce a bias making appear the patterns we did indeed observe.

Despite a high variability in species coexistence which was usually observed between different sites or between different communities (Zobel 1997), our results indicated that genera differed in the level of interspecific coexistence of their constituent species. This may

imply that the mean numbers of coexisting species may be phylogenetically conserved within genera. In fact, this quantitative biotic niche (many or few locally coexisting species) seems to be conserved no less than the abiotic niche (appendix IV.S1 as compared to Prinzing et al. 2001). In addition, we found that genera composed of high-coexistence species were young, independently of the ecological strategy and the occupied environments. This may indicate that species within older genera may be subject to lower biotic interactions. To our knowledge this phenomenon was never demonstrated before. Future explanations of this phenomenon will require phylogenetic reconstructions of coexistence or the analysis of large numbers of fossil communities across large numbers of clades.

The observed conservation of the mean numbers of coexisting species of clades may have implications for conservation of biological diversity. It is increasingly appreciated that present-day species decline is phylogenetically non-random: disappearing species tend to be clustered on particular branches of the tree of life. Thus species decline leads to the disappearance of entire major phylogenetic clades dating back dozens of millions of years (Mace et al. 2003). This has usually been explained by the fact that endangered clades tend to live in endangered types of habitats. Our results indicate that particular phylogenetic clades may also tend to live in communities where they coexist with many other species. Such clades of high-coexistence species might hence be particularly threatened by erosion of species diversity within local communities. In other words, even if we preserve all types of habitats we might still loose entire branches of the phylogenetic tree due to the ongoing erosion of local diversity within patches of each habitat type.

The mean numbers of coexisting species of genera decreased with their environmental tolerance or preference to luminosity, heat, soil moisture, soil nitrogen content and soil acidity. This variation in interspecific coexistence of genera along environmental gradients was different from the known variation in richness of the regional species pools along the

same gradients (e.g. Ewald 2003 for soil pH, and results not shown). These results suggested that extreme abiotic environments (i.e. high or low luminosity, temperature, soil moisture, soil nitrogen content and soil pH) may either promote or prevent species coexistence and that intermediate environments occupied by genera may imply intermediate numbers of coexisting species. This is not consistent with the common hypothesis that species richness in plant communities decreases with environmental severity (Grime 1977), but supports the hypothesis that species richness may be increased by positive interactions (e.g. facilitation) under stressful conditions (Michalet et al. 2006). We extend this hypothesis to patterns of interspecific coexistence of species within genera.

A common hypothesis about competition's role in community assembly is that the more competitive species may more easily displace competitors, limiting their coexistence with other species. Conversely, the very poor competitors may be frequently displaced and may coexist little, too. Overall, coexistence with numerous species should occur in species which have intermediate competitive ability (Goldberg & Barton 1992). Similarly, species coexistence has been considered to be increased by intermediate levels of disturbance (intermediate disturbance hypothesis – Shea et al 2004). We confirmed these hypotheses for the mean numbers of coexisting species of genera, when the roles of competitiveness and disturbance tolerance were considered independently. However, these hypotheses were rejected by our multivariate analysis, which showed that genera composed of high-coexistence species are those with highest competitive capacity and disturbance tolerance. This suggests that the apparent negative effect of very high competitiveness on interspecific coexistence in univariate analysis may in fact result from a simultaneous decrease of ruderalness.

We found only three significant relationships between coexistence level and trait variability (out of which one was impossible to confirm or refute in multiple regression

analysis including environmental conditions) and we will discuss them below. One explanation for this partial absence of relationships may be that species coexistence does not perfectly reflect biotic interactions. Some species may coexist in a given environment, but may have drastically different realized niches and may thus poorly interact (Cipriotti & Aguiar 2009). Moreover, we only measured coexistence between plant species, without considering, for instance, plant-insect or plant-phytophage interactions. These biotic interactions may strongly influence patterns of species coexistence and trait variability (Bascompte & Jordano 2007; Johnson et al. 2010). Another explanation, however, may be that the link between trait variability and biotic interaction is more complicated than we believed (see Introduction). Trait variability might not only increase due to intermediate levels of interaction, but also due to lowest levels of interaction (intraspecific coexistence, see below). A final explanation may be that the coexistence with on average a limited number of species in local communities is not equal to coexistence with a limited number of species across all localities of a region. These two measures of species coexistence may be considered separately in future analyses.

The significant hump-shaped relationships between trait variability and the level of interspecific coexistence within genera indicated that moderate biotic interactions with a moderate number of partners may promote trait variability within genera. This intermediate number of coexisting species may render species interactions important without being unpredictable (Urban et al. 2008). For example, species which coexist with a moderate number of competitors, natural enemies or mutualists may easily maintain (or evolve) different trait attributes in order to mediate these predictable interactions. Conversely, species which coexist with a very low number of other species (i.e. in monoculture) may maintain (or evolve) only a single trait attributes to this unique biotic interaction. Finally, species which coexist with a very large number of other species may maintain (or evolve) a single

opportunistic trait attribute permitting to mediate many unpredictable biotic interactions. Examples of such general-purpose opportunistic traits include highly plastic traits (Canale & Henry 2010) or little specialized structures (e.g. flowers, Navarro et al. 2004; Cuautle & Thompson 2009). Overall, a species coexisting with an intermediate number of species might hence succeed with either of many different trait states, and a clade composed of such intermediate coexistence species might hence establish a large variability of trait states.

For seed mass the relationship between level of interspecific coexistence and trait variability within genera was linear and negative (when environment was accounted for). This relationship is consistent with the hypothesis that one possible strategy to avoid competitive exclusion from a high number of coexisting competitors is to converge in trait attributes (Scheffer & van Nes 2006; Mayfield & Levine 2010). In fact, being sufficiently different to avoid competitors may be difficult to achieve for traits that are highly conserved within genera, such as seed size (refer to Appendix IV.S1). The best strategy to avoid competitive exclusion may hence consist in being sufficiently similar to coexisting species, which may lead to convergence of traits within genera of species choosing this strategy. On the other hand, the two traits that are least conserved within genera (life span and flowering duration) may in fact be those where being sufficiently dissimilar to coexisting species is most feasible, resulting in the maintenance of multiple trait states within genera.

VI. Conclusion

This study demonstrated that the level of local interspecific coexistence is conserved within clades. Erosion of local species diversity may hence threaten entire clades. Increased levels of interspecific coexistence reflect the combined effect of the competitive ability, disturbance tolerance and particular abiotic extremes. Clades showing highest levels of species coexistence show reduced variability of some traits, possibly because highest coexistence may

render species interactions unpredictable or it may induce convergence of trait states by competitive exclusion. The precise relationship between levels of coexistence of clades and their trait variability might depend on the degree to which traits are conserved within clades. Maintenance of functional diversity within clades across a region may hence depend on the number of species with which the clades' constituent species locally coexist (see also Thompson 2005). Local coexistence in more or less ephemeral habitat patches may thus have distinctly non-ephemeral consequences. If consistent in time and across regions, the maintenance of high trait variability in clades with intermediate levels of species coexistence might even result in increased trait diversification. We suggest testing this hypothesis in future research.

VII. Acknowledgments

Our study profits from the efforts of hundred of researchers to describe life-history traits, species coexistence, environmental distribution and phylogenetic classification of plant species throughout many decades. MH was supported by a PhD grant from Ministry of Research and Education (France), MH, IB and FH by an ATIP grant from CNRS.

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IX. Supporting information

Appendix IV.S1 Variability of species coexistence and life history traits explained across Angiosperm taxonomy.

Appendix IV.S2 Method to correct trait variability within genera for species richness of genera.

Appendix IV.S3 Method to estimate the age of genera.

Table IV.S1 Definitions of the extremes of the abiotic environmental gradients.

Appendix IV.S1 Variability of species coexistence and life history traits explained across Angiosperm taxonomy

We verified at which taxonomic level species coexistence varied most strongly, by partitioning the variance in species traits at different levels of Angiosperm taxonomy. To do so, we applied a variance components analysis (method of restricted maximum likelihood; StatSoft 2010) in order to estimate at which level of Angiosperm taxonomy species coexistence is determined. Levels of taxonomic hierarchy were between-orders, between-families, between-genera and species-within-genera (Smith et al. 2006; Bremer et al. 2009). This method has proven to be robust and to give similar results as methods using phylogenetic information (Prinzing et al. 2001). A maximum variance in species coexistence at the level of species-within-genera, for instance, indicates that species coexistence varies most within genera and thus differences in within-genus variabilities capture a major part of the variability of species coexistence. We applied the same approach to verify at which taxonomic level life history traits varied most strongly.

The variance components analysis showed a maximum of variance in species coexistence explained at the level of species-within-genera. Moreover, the variance components analysis showed a maximum of variance in species trait explained at the level of species-within-genera for all of the studied traits, except seed mass for which the maximum of variance was found at the level of families within orders (Table AIV.S1).

Table AIV.S1 Variance components analysis in species coexistence and trait attributes across angiosperm taxonomy. Data points are species, and percentage of variance explained at species level represents hence the variance unexplained by the analysis.

Variable	Percentage of variance explained			
	Species	Genus	Family	Order
Species coexistence	41.9	25.1	14.0	19.0
Begin of flowering	40.1	28.8	20.3	10.8
Duration of flowering	82.0	8.9	0.00	9.0
Life span	61.0	18.2	17.2	3.6
Seed mass (log)	0.6	3.3	95.1	1.1
Stress tolerance	66.7	14.8	14.8	3.7
Type of reproduction	55.8	0.4	16.5	9.2
Mean	51.0	12.4	27.3	6.2

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Appendix IV.S2 Method to correct trait variability within genera for species richness of genera

The observed variabilities within genera suffered from sample size bias: genera with a very small number of species showed lower variabilities than larger genera (even after randomizing species across genera). We thus corrected the observed variabilities by calculating their difference from the mean variabilities of a null model. The null model was created by reshuffling the species across genera 500 times (PopTools 3.1, www.cse.csiro.au/poptools/). This correction effectively suppressed any correlation to numbers of species per genus (Appendix III.S3). Note that our aim was not to estimate the significance of this difference between observed variabilities and null-mean variabilities. This would require additional division of the difference by the SD of the null model. However, as SD between samples (here: genera) increases when the size of the samples decreases, division by null-SD re-introduced a strong correlation to numbers of species per genus (Appendix III.S3). We thus corrected our observed trait variability by only calculating the difference between observed variability and the mean of the corresponding null variabilities.

Appendix IV.S3 Method to estimate the age of genera.

This appendix is identical to Appendix III.S1 in Chapter III.

To estimate ages of genera from the European angiosperm flora, we first reconstructed phylogenetic relationships in all angiosperm genera for which information was available. For each of the 554 genera, DNA sequences for at least one representative species were found in GenBank (http://www.ncbi.nlm.nih.gov). We searched GenBank for the five genes most commonly used in published phylogenetic studies of angiosperms from both chloroplast (*ndh*F, *mat*K, *rbc*L and *trn*L-*trn*F), and nuclear genomes (ITS1-5.8S-ITS2). To avoid large regions of missing data in our sequence matrices, we first created a matrix of rbcL sequences for 215 genera (*Amborella trichopoda* was included as outgroup), which was used to reconstruct phylogenetic relationships for all families in our sample and to estimate ages of splits between sister pairs of families. The sequences were selected so that each small family (less than five genera) was represented by all genera in the sample, and large families were represented by at least four genera each. Phylogenetic analyses within 24 large families (five genera and more) in our sample were performed separately for 21 sub-tree (in three cases two families were combined in a sub-tree), for which different sets of genes could be compiled from the Gene Bank (Table AIV.S1a).

We used Bayesian analysis (Rannala & Yang 1996; Yang & Rannala 1997) to estimate and search for phylogenies in all of our samples (the large sample of genera representing all families, the „family tree“, and the 21 sub-clades representing large families) by application of MrBayes 3.1.2 software (Ronquist & Huelsenbeck 2003). All data matrices were first tested against 56 models of DNA evolution in PAUP* 4.0 (Swofford 2002) and resulting scores were used to select models, which best fit the data. Our selection was based on the Akaike Information Criterion (AIC) (Akaike 1974) as implemented in ModelTest 3.7 (Posada

& Crandall 1998). The results of these analyses were used to create input files for MrBayes3.1.2, so that for each gene partition the closest model settings available in the program were specified. To allow estimation of substitution parameters for each region of DNA separately, we decoupled parameter estimation across the datasets. The Bayesian searches were based on $2.0*10^5$ to $4.0*10^6$ generations (Table AIV.S1a) with Markov chain Monte Carlo (MCMC) starting from random trees and vague priors (program‘s defaults). Trees were sampled every 100th or 1000th generation (depending on the total number of generations), providing from 2000 to 4000 trees in each of runs (for each data set at least two runs were used to confirm that they converged on similar stationary parameter estimates). The stationary (post burn-in) phase was determined in each analysis based on the average standard deviation of split frequencies (Huelsenbeck & Ronquist 2001) which are reported in Table AIV.S1a. The post burn-in trees were used to reconstruct a majority-rule consensus tree for each data set.

Divergence times among genera in a majority-rule consensus phylogram of the “family tree” (the tree with 215 representative genera of all families) were estimated using the Penalized Likelihood method (PL) of Sanderson (2002) using the software r8s version 1.70 (Sanderson 2004). We applied the Truncated Newton algorithm with bound constraints, which can handle age constraints and uses gradients for better convergence of rates. The outgroup taxon (*Amborella trichopoda*) was pruned prior to analysis. We used published age estimates for divergences at the base of the tree (Bremer 2000; Wikström et al. 2001; Bremer et al. 2004; Janssen & Bremer 2004; Moore et al. 2007) as fixed age constraints (Table AIV.S1b). Cross-validation was undertaken on the consensus tree to select an optimal smoothing value (Sanderson 2002). The analysis resulted in a chronogram with estimated ages of divergences among all families and among genera in small families.

As a next stage of our dating analyses, we reconstructed dated phylograms (chronograms) for all 24 large families in our sample, represented in the 21 sub-clades. The majority-rule consensus trees resulting from each of the Bayesian analyses (Table AIV.S1a) were further used in PL dating analyses, as described above. We used age estimates from our dating analyses on the "family tree" to provide the stem node age for each of the 21 tree as fixed age constraint in PL analyses. The analyses resulted in chronograms, from which both stem and crown node age estimates for all genera could be retrieved.

Table AIV.S3a Statistical results of Bayesian phylogenetic reconstructions of the "family tree" and within the largest families of angiosperms from the data set of Central European flora. Under N are numbers of clades. Numbers of terminal taxa include outgroups. In all analyses of the clades nuclear genome was represented by ITS sequences.

N	Family	Likelihood	STDev	PSRF	N taxa.	N gen.	cpDNA loci
1	Asteraceae	12093.0	0.014	1.008	55	$4.00*10^6$	rbcL
2	Apiaceae	9137.3	0.009	1.001	31	$1.25*10^6$	rbcL
3	Boraginaceae	6941.5	0.009	1.000	10	$1.00*10^6$	rbcL, trnL-trnF, atpß
4	Brassicaceae	20477.9	0.013	1.002	39	$1.00*10^6$	ndhF, matK
5	Campanulaceae	5636.4	0.007	1.000	7	$1.00*10^6$	rbcL, ndhF
6	Caryophyllaceae / Chenopodiaceae	16383.4	0.019	1.000	36	$3.00*10^6$	rbcL, matK
7	Cyperaceae	6913.6	0.009	1.000	14	$1.25*10^6$	rbcL, trnL-trnF
8	Dipsacaceae	12105.5	0.001	1.002	13	$1.00*10^6$	rbcL, ndhF
9	Ericaceae / Primulaceae	25438.8	0.002	1.000	19	$5.00*10^5$	rbcL, ndhF, matK
10	Fabaceae	15693.2	0.008	1.000	24	$1.25*10^6$	rbcL, matK
11	Gentianaceae	6390.9	0.004	1.000	7	$2.00*10^5$	rbcL, matK
12	Lamiaceae / Scrophulariaceae	13847.8	0.010	1.002	46	$2.50*10^6$	rbcL, trnL-trnF
13	Liliaceae	13961.9	0.006	1.000	20	$1.00*10^6$	rbcL, matK
14	Malvaceae	4707.4	0.001	1.000	5	$1.00*10^6$	rbcL, ndhF
15	Orchidaceae	12823.9	0.004	1.000	18	$1.00*10^6$	rbcL, matK, rpl16
16	Papaveraceae	7065.9	0.016	1.000	8	$1.25*10^6$	rbcL, trnL-trnF, rps16
17	Poaceae	20793.7	0.016	1.000	62	$1.50*10^6$	rbcL, matK
18	Ranunculaceae	14260.3	0.005	1.007	17	$1.00*10^6$	rbcL, matK, trnL-trnF
19	Rosaceae	13481.3	0.019	1.001	22	$1.00*10^6$	rbcL, matK
20	Saxifragaceae	7259.1	0.001	1.000	7	$5.00*10^5$	rbcL, matK
21	Solanaceae	8436.1	0.006	1.000	7	$1.00*10^6$	rbcL, matK, ndhF
	All-families tree	39995.6	0.018	1.003	215	$1.50*10^6$	rbcL

Table AIV.S3b Node age estimates from earlier studies used for calibration of the "family tree" of angiosperms from Central Europe. Under N are numbers of nodes.

N	Taxon	Node	Age	Reference
Fixed ages:				
1	Nymphaeales	stem	164	Moor *et al.* 2007
2	Mesangiosperms	crown	144	Moor *et al.* 2007
Monocots:				
3	Acoraceae	stem	134	Bremer 2000
4	Alismatales	crown	128	Janssen and Bremer 2004
5	Core_Monocots	crown	126	Janssen and Bremer 2004
6	Orchidaceae	stem	119	Janssen and Bremer 2004
7	Araceae	crown	117	Janssen and Bremer 2004
8	Poales	stem	117	Janssen and Bremer 2004
9	Butomaceae	stem	88	Janssen and Bremer 2004
10	Cyperaceae	stem	88	Janssen and Bremer 2004
11	Zosteraceae	stem	47	Janssen and Bremer 2004
Eudicots:				
12	Euasterids	crown	123	Bremer *et al.* 2004
13	Aquifoliales	stem	121	Bremer *et al.* 2004
14	Ericales	crown	114	Bremer *et al.* 2004
15	Apiales	stem	113	Bremer *et al.* 2004
16	Cornales	crown	112	Bremer *et al.* 2004
17	Asterales	stem	112	Bremer *et al.* 2004
18	Gentianales	stem	108	Bremer *et al.* 2004
Minimal ages:				
19	Malpighiales	stem	90	Moor *et al.* 2007
20	Fagales	stem	84	Wikström *et al.* 2001
21	Fabales	stem	60	Moor *et al.* 2007

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Table IV.S1 Definitions of the extremes of the environmental gradients*.

This appendix is identical to Table III.S1 in Chapter III.

Environmental gradients	Extremes	Definitions
Luminosity (L)	1	Plants are in deep shade, may be less than 1%, seldom more than 30% full light irradiance intensity
	9	Plants are in full light, found mostly in full sun, rarely with less than 50% irradiance intensity
Temperature (T)	1	Plants are found only in high mountains (or in boreal-arctic regions), mostly in alpine and nival levels
	9	Plants grow in extremely warm conditions, spreading from the Mediterranean only into the warmest places of the upper Rhine valley
Continentality (C)	1	Plants grow in extremely seasonally constant temperature, only in few outposts in Central Europe
	9	Plants grow in extremely seasonally variable temperature, virtually absent from western central Europe
Soil moisture (M)	1	Extremely dry soils, e.g. bare rocks or sand
	12	Submerged plants, permanently or almost constantly under water
Soil reaction (R)	1	Plants grow in extreme acidity, never found on weakly acid or basic soils
	9	Lime indicators, always found on calcareous soils
Soil nitrogen (N)	1	Plants grow only in soils very poor in mineral nitrogen
	9	Plants are indicators of soils extremely rich in mineral nitrogen, such as cattle resting places, or near polluted rivers

* Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992). *Zeigwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica, Göttingen.

Conclusions & Perspectives

Pour comprendre les processus d'ajustement des traits aux contraintes de l'environnement, les recherches se sont essentiellement focalisées sur l'étude de la moyenne des attributs de traits (Thuiller et al. 2004a ; Ackerly & Cornwell 2007), de la variabilité phénotypique intraspécifique (Reich et al. 2003 ; Albert et al. 2010) et de la variabilité interspécifique au sein des communautés (De Bello et al. 2009). Ces recherches ont permis de mieux comprendre les réponses fonctionnelles des organismes aux contraintes environnementales, à l'échelle des individus (Larcher 2003), des espèces (Grime 1977 ; Ellenberg 1988 ; Lavorel et al. 1997 ; Smith et al. 1997 ; Westoby 1998), des communautés (Ricklefs & Travis 1980 ; Stevens et al. 2003 ; Ackerly & Cornwell 2007 ; Swenson & Enquist 2007) et des lignées évolutives (Moles et al. 2005 ; Westoby et al. 2002 ; Wright et al. 2007 ; Prinzing et al. 2008 ; Cavender-Bares et al. 2009).

Cependant, la nature complexe des réponses phénotypiques aux variations environnementales n'est pas encore entièrement comprise. Des études en conditions contrôlées ont montré que les interactions complexes entre traits (intégration phénotypique) et entre conditions environnementales occupées par les espèces (intégration environnementale) peuvent grandement influencer la valeur moyenne et la variabilité de leurs traits (Levins 1968 ; Gianoli & Palacio-Lopez 2009). Ces études ont notamment montré que l'intégration phénotypique est fortement contrôlée par les conditions abiotiques et peut alors limiter la capacité des espèces à répondre aux variations de l'environnement (Schlichting 1989b). Cependant, l'influence des conditions abiotiques et biotiques sur l'intégration phénotypique et environnementale n'a été que très peu étudiée en conditions naturelles (pour l'intégration phénotypique, voir Reich et al. 2003) et son implication sur les caractéristiques biologiques et écologiques des espèces est peu connue. De même, la plupart des études sur la réponse des

traits et l'environnement ne prennent pas en compte le fait que la variabilité des traits peut différer entre les clades (visible au sein de chaque flore ou faune, par exemple Jäger & Werner 2002). Pourtant, nous ignorons à peu près complètement les raisons pour lesquelles, au sein d'une région, certains clades ont des traits beaucoup plus variables que d'autres clades.

Ce travail avait pour objectif d'élargir les connaissances sur les processus de réponse des traits à l'environnement aux niveaux intra- et interspécifiques. Au niveau intraspécifique, il s'agissait d'abord d'estimer les conséquences écologiques d'une forte intégration phénotypique et d'évaluer son influence sur d'autres paramètres plus classiques, tels que la moyenne des attributs de traits. Nous avons ensuite développé une approche multi-spécifique afin de déterminer si une forte intégration phénotypique et environnementale peut être un facteur contribuant à l'endémisme de certaines espèces. Au niveau interspécifique, nous avons commencé par étudier le rôle de l'environnement abiotique dans la variabilité des traits réalisée au sein des clades. Enfin, nous avons cherché à déterminer les facteurs influençant le niveau de coexistence interspécifique au sein des clades et le rôle de ces interactions biotiques potentielles sur la variabilité des traits. Dans cette dernière partie, nous commencerons par exposer les principales conclusions que nous tirons de nos résultats. Nous intégrerons ensuite ces résultats dans des perspectives de recherches.

I. Conclusions générales

I.1. Intégration phénotypique et environnementale

Dans le chapitre I, nous avons étudié le changement le long d'un gradient naturel d'altitude de la taille moyenne des plantes, la production moyenne de graines, les stratégies moyennes de croissance et de reproduction et l'intégration phénotypique chez le Chou de Kerguelen (*Pringlea antiscorbutica*), à petite et à grande échelles spatiales (Fig. 7). Nous avons montré

que l'augmentation de l'intégration phénotypique avec le stress abiotique qui avait été observée en milieu simplifié lors d'expériences en serre (Schlichting 1989a, b; Waitt & Levin 1993; Sleeman et al. 2002; Gianoli 2004; Pigliucci & Kolodynska 2006) se produit également dans le milieu naturel. Nous avons également montré que le changement de l'intégration phénotypique avec l'environnement se produit à plus petite échelle spatiale que le changement dans la moyenne des traits, révélant un aspect nouveau de la réponse phénotypique complexe d'une plante à l'environnement (Richards et al. 2005). Enfin, nous avons montré que l'intégration phénotypique pourrait contraindre le changement de paramètres plus classiques, comme la moyenne des attributs de traits, ce qui souligne l'importance de prendre en compte l'intégration phénotypique dans les études de variation des traits des espèces.

Le changement dans les stratégies de croissance et de reproduction du Chou de Kerguelen avec l'altitude constitue essentiellement une réponse à la plus forte compétition intra- et interspécifique à basse altitude et aux fortes contraintes abiotiques de haute altitude. Cependant, ce changement dans les stratégies ne semble pas suffire à compenser les effets de l'altitude sur les plantes : la croissance et la reproduction diminuent avec l'altitude. Les stratégies de croissance et de reproduction semblent contraintes par la plus forte intégration phénotypique sous les conditions abiotiques stressantes de haute altitude. Ceci suggère que le Chou de Kerguelen n'aurait actuellement pas la flexibilité phénotypique suffisante pour supporter des conditions environnementales plus stressantes. Une limitation de sa gamme de tolérance environnementale aux conditions subantarctiques typiques, froides et humides, a déjà été suggérée chez le Chou de Kerguelen en raison de sa haute sensibilité à la sécheresse (Hennion 1992; Chapuis et al. 2004; Hummel et al. 2004), mais aussi aux fortes températures et salinités (Hennion & Martin-Tanguy 2000, Dufeu et al. 2003, Hummel et al. 2004). La forte intégration phénotypique du Chou de Kerguelen en condition abiotique stressante est un

nouvel élément pour expliquer la haute sensibilité de cette espèce aux changements des conditions abiotiques.

Les résultats obtenus sur le Chou de Kerguelen appuient notre hypothèse qu'une plus forte intégration phénotypique et environnementale pourrait influencer la distribution écologique d'une espèce et pourrait notamment contribuer à l'endémisme. Nous avons testé cette hypothèse dans le chapitre II par l'étude de 14 espèces de plantes présentes sur les Iles Kerguelen et dont la distribution géographique variait du strict endémisme jusqu'à une répartition mondiale (Lourteig & Cour 1963 ; Walton 1979 ; Edgar 1986 ; Frenot et al. 2001 ; Van der Putten et al. 2010). Nous avons montré que les espèces endémiques sont davantage restreintes aux habitats stressants et peu compétitifs de haute altitude. De plus, l'intégration phénotypique, l'intégration environnementale et les corrélations entre les traits et l'environnement augmentent avec le niveau d'endémisme des espèces (Fig. 7). Nos résultats démontrent la contribution de l'intégration phénotypique et environnementale à la distribution géographique des espèces.

Nos résultats appuient également les hypothèses émises par certains auteurs pour expliquer l'endémisme et en suggèrent certains mécanismes. Premièrement, ils apportent de forts arguments écologiques en faveur d'un endémisme qui résulterait de la restriction croissante de l'habitat des espèces au cours du temps (*paleoendemism*, Stebbins & Major 1965). Nos résultats confortent ainsi l'hypothèse d'une histoire ancienne des espèces endémiques dans la région subantarctique (Van der Putten et al. 2010). Deuxièmement, la restriction des espèces endémiques aux habitats de haute altitude fournit un nouvel argument à l'hypothèse selon laquelle les espèces endémiques se limitent aux habitats stressants afin d'échapper à la compétition (Gankin & Major 1964 ; Lavergne et al. 2003, 2004). Enfin, ces résultats indiquent que les espèces endémiques n'auraient pas la flexibilité phénotypique suffisante pour étendre leur gamme écologique. C'est un nouvel élément explicatif de patterns

déjà connus : une spécialisation des espèces endémiques à leur habitat (Stebbins 1980) et l'existence d'un compromis entre distribution géographique et performance (Sultan et al. 1998 ; Caley & Munday 2003 ; Richards et al. 2005).

Nos résultats suggèrent également que la haute sensibilité des espèces endémiques aux changements climatiques (Hennion 1992; Chapuis et al. 2004; Hummel et al. 2004) pourrait résulter d'une disparition des combinaisons environnementales particulières pour lesquelles ces espèces sont spécialisées. Nos résultats ont donc des implications majeures pour la conservation de la flore subantarctique.

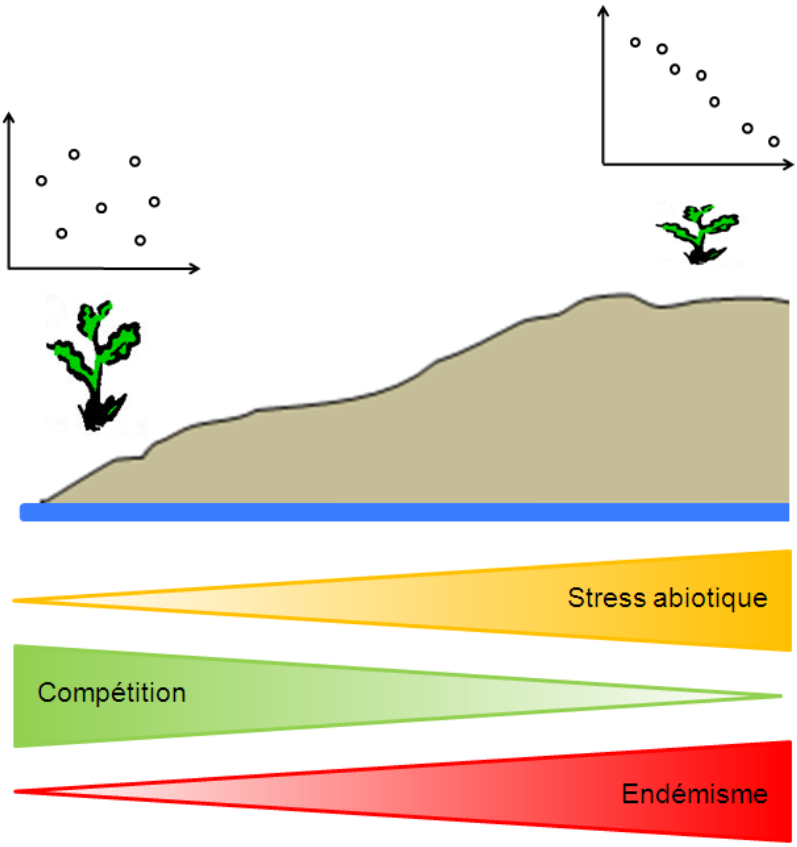

Figure 7 Représentation schématique des conclusions principales des chapitres I et II. Les changements à grande échelle spatiale dans la forme des plantes et leur stratégie de croissance et de reproduction avec l'altitude dépendent des gradients opposés de compétition et de stress abiotique. Les changements dépendent également d'une augmentation de l'intégration phénotypique avec l'altitude à petite échelle spatiale. Enfin, les espèces présentent une plus grande intégration phénotypique et environnementale, ainsi que de plus fortes corrélations entre les traits et l'environnement. Elles semblent spécialisées aux conditions stressantes et peu compétitives de haute altitude, mais peu flexibles à un changement des conditions environnementales.

I.2. Variabilité des traits réalisée au sein des clades

Nous savons que les clades au sein d'une région présentent, à l'époque actuelle, des niveaux différents de variabilité phénotypique réalisée, comme il est indiqué par de nombreux exemples dans chaque flore ou faune (Jäger & Werner 2002). Cette variation est un aspect majeur, mais très peu abordé, de la biodiversité. Dans le chapitre 3, nous avons étudié la variabilité phénotypique réalisée au sein des genres d'Angiospermes de l'Europe Centrale. Nous avons montré que la variabilité ne dépend pas de l'âge des genres, mais de la position qu'ils occupent le long des gradients abiotiques. Plus précisément, la variabilité phénotypique réalisée au sein des genres est plus grande lorsqu'ils occupent des positions intermédiaires le long des gradients. De plus, les patterns de variabilité des traits le long des gradients abiotiques au sein des genres sont différents de ceux qui existent au sein du pool d'espèces. Nous avons également montré que cette plus grande variabilité au centre des gradients abiotiques correspond à une plus grande indépendance des traits des espèces avec les facteurs abiotiques.

Ces résultats indiquent un rôle de la position d'un genre dans l'environnement abiotique sur la variabilité de ses traits en réponse à des opportunités environnementales inhérentes aux espèces de ce genre (Fig. 8). Un environnement abiotique donné pourrait par exemple contenir un grand nombre de compétiteurs du même clade ou pourrait contenir les phytophages ou pollinisateurs spécialisés d'un clade. Ces environnements favoriseraient l'établissement et le maintien de hauts niveaux de variabilité de traits dans les clades qui les occupent, sans augmenter la variabilité des traits dans le pool d'espèces correspondant.

Deux explications complémentaires des patterns sont possibles. Premièrement, les conditions abiotiques extrêmes peuvent former des filtres environnementaux étroits permettant uniquement l'établissement des espèces d'un clade qui partagent des traits particuliers (à l'échelle des communautés locales : Helmus et al. 2007b). Cette origine

possible des patterns est bien illustrée dans notre étude par le fait que la diminution de la variabilité des traits au sein des clades vers les extrêmes des gradients abiotiques correspond à une plus grande corrélation entre les traits des espèces et les facteurs abiotiques. Deuxièmement, les environnements abiotiques intermédiaires peuvent abriter un plus grand nombre d'espèces en interaction (Welden & Slauson, 1986). Les filtres et les sélections biotiques diverses, en particulier la compétition, pourraient permettre le maintien (voire l'émergence) d'une plus grande variabilité des traits au sein d'un clade (voir aussi Dodzhansky 1950; Fisher 1960; MacArthur 1969). Nous avons testé cette hypothèse dans le chapitre IV, en étudiant le rôle de la coexistence interspécifique des plantes dans la variabilité des traits au sein des clades.

Dans le chapitre IV, nous avons d'abord comparé le niveau de coexistence interspécifique (nombre moyen d'espèces de plantes en coexistence avec une espèce donnée) entre les genres d'Angiospermes des Pays-Bas. Nous avons montré que les clades diffèrent significativement dans leur niveau de coexistence, ce qui indique que les espèces de certains clades coexistent avec beaucoup d'espèces alors que les espèces d'autres clades coexistent avec peu d'espèces, i.e. poussent pratiquement en monoculture. C'est la première fois qu'une telle conservation des niveaux de coexistence interspécifique au sein des clades d'une région est montrée. Elle implique que l'érosion de la richesse d'espèces en coexistence dans des communautés locales risque de mettre en péril des clades entiers.

Dans le chapitre IV, nous avons ensuite quantifié le rôle de la coexistence interspécifique sur la variabilité phénotypique réalisée au sein des clades. Nous montrons d'abord que le niveau de coexistence interspécifique des clades évolue linéairement le long des gradients abiotiques. Ceci indique que les environnements abiotiques extrêmes sont favorables soit aux coexistences importantes soit aux coexistences faibles (Fig. 8). Les conditions abiotiques intermédiaires seraient favorables à des genres dont le niveau de coexistence est

intermédiaire. Si nous rapprochons ces résultats de ceux du chapitre III, nous pouvons suggérer que des niveaux de coexistence intermédiaires favorisent la variabilité des traits au sein des genres. C'est effectivement ce que nous observons pour deux traits (durée de la floraison et durée de vie des plantes). Ces résultats suggèrent que les niveaux de coexistence intermédiaires seraient favorables à des interactions biotiques diverses mais toujours spécifiques avec des partenaires prévisibles. Des espèces en coexistence modérée pourraient davantage prospérer si elles présentent l'un des attributs de traits qui permettent de faire face à une ou plusieurs de ces interactions biotiques prédictibles. Un clade dont les espèces sont en coexistence modérée pourrait ainsi établir ou maintenir une grande variabilité d'attributs de traits (Fig. 8).

Les deux traits mentionnés ci-dessus sont particulièrement peu conservés au sein des genres et des niveaux taxinomiques supérieurs. Par contre le trait le plus conservé est la masse des graines. Pour ce trait on observe une diminution de la variabilité avec le niveau de coexistence des espèces d'un genre (quand la position environnementale est associée en co-variable). Cela appuie l'hypothèse que la compétition accrue au sein des genres occupant des niches similaires peut induire une convergence des traits (Mayfield & Levine 2010). Une telle convergence forte assure une compétition symétrique et réduit donc la probabilité d'une exclusion compétitive. Ceci est particulièrement important pour des traits fortement conservés pour lesquelles une divergence suffisamment forte est difficile à établir (Scheffer & van Nes 2006). La relation précise entre les niveaux de coexistence des clades et la variabilité de leurs traits pourrait ainsi dépendre du degré de conservation des traits à l'intérieur des clades. De manière générale, la coexistence locale, qu'elle soit éphémère ou non, pourrait donc avoir des conséquences sur la variabilité de certains traits à l'intérieur des clades au long terme. Ces patterns macro-évolutifs s'accordent avec l'hypothèse de la mosaïque géographique de co-

évolution (« *Geographic mosaic of coevolution hypothesis* », Thompson 2005), qui n'a été testée qu'au niveau micro-évolutif sur des paires d'espèces en interaction locale.

Les résultats des chapitres III et IV indiquent que les environnements abiotiques intermédiaires jouent un rôle important dans l'émergence d'une grande variabilité de traits au sein des genres, à travers le maintien de niveaux de coexistence interspécifiques intermédiaires. La préservation de ces environnements abiotiques intermédiaires, ainsi que de la diversité spécifique qu'ils comportent, apparaît donc comme essentielle pour le maintien de la variabilité fonctionnelle dans les clades et dans les écosystèmes.

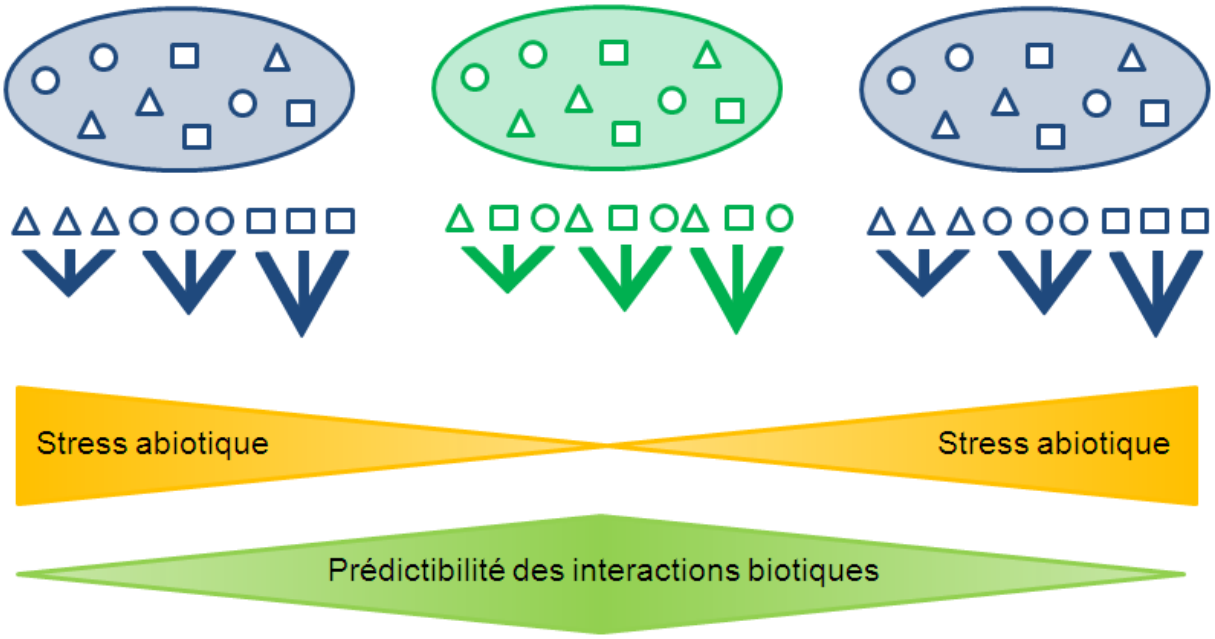

Figure 8 Représentation schématique des conclusions des chapitres III et IV. La variabilité des traits au sein des genres diminue vers les extrêmes abiotiques et augmente en milieu abiotique intermédiaire. Cette relation entre la variabilité des traits et l'environnement abiotique résulterait des opportunités environnementales inhérentes aux espèces d'un même clade. L'augmentation de la variabilité en conditions abiotiques intermédiaires serait potentiellement due à une plus grande prédictibilité des interactions biotiques dans ces milieux.

II. Perspectives

Ce travail nous amène à émettre quelques hypothèses qu'il serait intéressant de tester pour de futures recherches.

II.1. Intégration phénotypique au sein des clades

Nous avons montré que la variabilité phénotypique réalisée au sein des genres diminue vers les extrêmes des gradients abiotiques et que cette diminution correspond à une plus grande corrélation entre les traits des espèces et les facteurs abiotiques. Cette diminution ne pourrait-elle pas également refléter une plus grande corrélation entre les traits des espèces du même genre ? L'existence de différentes stratégies chez les espèces de plantes est observée depuis longtemps (Grime 1977). Plus récemment, des auteurs ont suggéré que ces stratégies résulteraient de la co-évolution de plusieurs traits à travers la phylogénie (Westoby 1998 ; Wright et al. 2007). Cette co-évolution des traits au sein des taxa peut être interprétée comme une forte intégration phénotypique (Reich et al. 2003 ; Pigliucci & Preston 2004). Cependant, la variation de l'intégration phénotypique au sein des clades d'une région entière le long de gradients abiotiques et biotiques n'a pas été testée. Nous pourrions vérifier si la force des corrélations entre les traits des espèces de l'Europe Centrale dépend de leur appartenance à certains clades, et notamment de la position de ces clades le long de gradients abiotiques et biotiques.

II.2. Héritabilité de l'intégration phénotypique

L'intégration phénotypique résulte en partie de contraintes génétiques internes (Waitt & Levin 1998), mais peut également refléter une faible plasticité phénotypique (Gianoli & Palacio-Lopez 2009). Il serait ainsi intéressant de vérifier si les changements d'intégration phénotypique avec l'altitude que nous observons au niveau intraspécifique chez le Chou de

Kerguelen (*Pringlea antiscorbutica*) sont d'origine génétique ou plastique. Pour cela, nous pourrions envisager des expériences de transplantation d'individus entre des sites d'altitudes variées. Une expérience pourrait aussi être menée en phytotrons sur des plantes issues de graines récoltées dans des populations situées à différentes altitudes. Nous pourrions élargir l'expérience à plusieurs espèces des îles Kerguelen de niveaux d'endémisme différents (projet de post-doc avec Sharon Robinson à l'Université de Wollongong, Australie).

II.3. Diversification des traits au sein des clades

Le rôle de l'environnement abiotique et biotique sur la variabilité des traits réalisée au sein des genres de l'Europe Centrale peut s'expliquer par des processus d'assemblage des espèces (Mayfield & Levine 2010), mais aussi par des processus de diversification des traits (Pfennig 2009). Nous ne sommes pas en mesure de distinguer ces deux mécanismes à travers nos résultats actuels. Pour cela, il nous faudrait mesurer le taux de diversification des traits au sein des taxa-frères en fonction de leur environnement abiotique et biotique ancestral à l'aide d'une analyse phylogénétique (Pavoine et al. 2010). Cependant, il est essentiel de travailler sur des lignées complètes pour correctement interpréter les patterns de diversification. Notre analyse nécessiterait donc de disposer d'une phylogénie globale qui dépasse l'Europe Centrale. De plus, cette phylogénie devrait être datée, ce qui est encore loin d'exister pour les genres d'Angiospermes à l'échelle globale. Il nous faudrait donc sélectionner des lignées nettement plus restreintes au sein des Angiospermes.

II.4. Rôle des interactions biotiques

Nous émettons l'hypothèse d'un rôle de la compétition sur (i) la forme élancée des plantes et la faible intégration phénotypique du Chou de Kerguelen à basse altitude et sur (ii) la restriction de la distribution moyenne des espèces endémiques aux conditions plus stressantes

de haute altitude. Notre connaissance de la végétation de basse et de haute altitude sur les Iles Crozet et Kerguelen laisse supposer l'existence d'une compétition plus importante à basse altitude. Cette forte présomption repose essentiellement sur une observation des parties aériennes de la végétation (végétation ouverte/fermée, abondance et recouvrement des espèces, Smith 1984). Il nous manque des informations sur la compétition au niveau racinaire. L'architecture racinaire de certaines espèces des Iles Kerguelen intervient dans leur capacité de colonisation (Frenot et al. 1998), et pourrait donc également influencer leur capacité compétitive. Une étude approfondie des interactions racinaires pourrait fournir de nouveaux éléments explicatifs de nos patterns à basse altitude.

Nos données de coexistence aux Pays-Bas (Schaminée et al. 1995–1999) nous ont permis d'estimer les interactions biotiques potentielles entre les plantes. Ces données nous ont permis de mettre en évidence certaines relations entre la variabilité phénotypique réalisée au sein des genres et le niveau de coexistence. Cependant, ces relations sont peu nombreuses et les patterns assez complexes. Nous pourrions d'abord envisager de compléter notre étude par des mesures de coexistence entre plantes et animaux (pollinisateurs, phytophages), ces interactions pouvant en effet influencer les traits des plantes (Díaz et al. 2007 ; Navarro et al. 2007 ; Johnson et al. 2010). Cependant, de telles données ne sont pas encore disponibles pour un grand nombre de genres de la région. Nous pourrions ensuite envisager de tester le rôle de la coexistence entre les espèces apparentées (c'est-à-dire appartenant au même genre ou à la même famille) sur la variabilité phénotypique réalisée au sein des genres. Les espèces apparentées sont supposées s'exclure davantage par compétition que des espèces éloignées (Darwin 1859, Webb et al. 2002). Cette coexistence entre espèces apparentées pourrait fournir des éléments nouveaux pour la compréhension de nos patterns de variabilité des traits.

II.5. Rôle du métabolome dans les patterns d'intégration phénotypique

L'intégration phénotypique au sein d'un organisme est en partie contrôlée par des contraintes internes génétiques et ontogéniques (Pigliucci & Preston 2004). Les métabolites sont des éléments régulateurs du phénotype (Keurentjes 2009), et interagissent étroitement avec l'environnement (Fiehn 2002). L'étude du métabolome pourrait fournir de nouveaux éléments explicatifs de nos patterns d'intégration phénotypique. Récemment, la composition biochimique en amines et en polyamines, régulateurs de croissance répondant aux stress abiotiques chez les plantes, a été étudiée chez neuf espèces autochtones des Iles Kerguelen (Hennion *et al.* soumis). Cette étude a montré que la composition biochimique en amines varie selon l'espèce et selon la lignée. Elle a également mis en évidence une variation de la composition biochimique entre des conditions abiotiques contrastées de manière cohérente entre les espèces. Cependant, cette étude ne permettait pas de quantifier le changement de la composition biochimique des espèces le long de gradients abiotiques. Elle ne permettait pas non plus de corréler le changement de la composition biochimique avec le niveau d'endémisme des espèces, ou avec leur niveau d'intégration phénotypique.

Nous disposons actuellement de données sur la composition biochimique en amines et en polyamines le long de trois gradients abiotiques chez quatorze espèces de plantes des Iles Kerguelen présentant des niveaux d'endémisme variés. Les mesures morphologiques associées aux mesures biochimiques chez ces quatorze espèces nous permettront de corréler les compositions en différents composés avec à la fois l'intégration phénotypique réalisée, les conditions abiotiques et le niveau d'endémisme des espèces. Ces analyses devraient conduire à une meilleure compréhension de la réalisation du phénotype d'une plante en réponse aux variations de son environnement naturel, permettant de cerner au plus près un ensemble de mécanismes internes, l'intégration phénotypique, dont on a pu apprécier la large portée écologique et biogéographique pour les espèces végétales.

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Annexe

Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France)

Hermant Marie, Lobry Jeremy, Bonhommeau Sylvain, Poulard Jean-Charles and Le Pape Olivier

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Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France)

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A.I. Abstract

The aim of the present study was to analyse the influence of warming on flatfish populations in the Bay of Biscay. 17 autumn cruises conducted from 1987 to 2006 over the whole shelf of the Bay of Biscay provided data for the abundance and occurrence of adults for twenty flatfish species. Trends in flatfish abundance were analysed with regard to geographic range of populations and interannual fluctuations in abundance were related to seawater temperature. Results showed significant trends in abundance and occurrence for 55% of the flatfish species in the Bay of Biscay. The response to warming of seawater was correlated to geographic ranges of species. While the abundance of the northern temperate species decreased, that of southern ones increased. Moreover, for 40% of the species which densities have significantly changed, abundances were correlated to temperatures in their year of birth, positively for southern species and negatively for northern ones. Last, the abundance of flatfish adults over the Bay of Biscay was compared to previous data on juveniles in the Bay of Vilaine, one of the estuarine nursery ground in this area. For the northern species which have disappeared, the decline in juvenile abundances preceded that of adults by several years, indicating that the recruitment is the process affected. We concluded on a major impact of warming to explain changes in flatfish species abundances. Nevertheless, the impact of fishing interacts with that of climate change because the exploited species appeared to be the most negatively affected.

Key-words: flatfish, temporal trends, interannual variability, climate change, geographic distribution, Bay of Biscay.

A.II. Introduction

The temperature of the upper 300 m of the North Atlantic increased by about 0.6 °C between 1984 and 1999, with substantial interannual variability (Brander et al. 2003). In the same way, longterm trends and interannual variations in abundances and distribution of fish have been observed over the past few years. Perry et al. (2005) showed a northward shift of fish species in the North Sea over the last 25 years, related to changes in seawater temperature. Other studies have related successive northward and southward migrations of fish species to alternating warming and cooling events of the North Atlantic seawater (Drinkwater 2005). Rose (2005) found that these changes in fish distribution linked to climate change in the North Atlantic depend on the physiological limits of species.

In addition to sea temperature, other factors, and especially exploitation, have to be taken into account when trying to explain changes in distribution and abundance of fishes: in their study on the commercial gadoid and flatfish species of the North Atlantic, Brander et al. (2003) demonstrated that the abundance of warmwater species in capture increased in comparison to colder water species and suggested that consequences of fishing overlay those of the seawater warming. On the other hand, Pauly (1994) and Van der Veer et al. (2003) suggested that the replacement of sub-polar species by tropical ones will result in higher occurrences of small flatfish species of less commercial interest.

The Bay of Biscay is an arm of the North Atlantic extending along the west coast of France down to the north coast of Spain (ICES Area VIIIa/c), located at the interface between the North Atlantic sub-polar and sub-tropical gyres. In this area, the seawater temperature in winter has significantly increased over the last century, with the fastest rate of prolonged change occurring in the last two decades. Moreover, this general trend does not appear to be slowing down (Koutsikopoulos et al. 1998; Garcia-Soto et al. 2002).

Poulard and Blanchard (2005) have investigated the relationship between seawater warming and species composition of the fish communities in the Bay of Biscay. They showed a change in species composition of fish communities, with an expansion of the subtropical and tolerant species and a decline of the temperate and boreal species. Désaunay et al. (2006) investigated changes in abundance of 4 selected commercial flatfishes with regard to their biogeographic distribution. They noted a regression of northern winter spawners such as plaice and dab, and an expansion of a southern summer spawner, the wedge sole. However, our understanding of the effects of climate change on fish populations is still hampered by the lack of long-term and in-depth analyses at the level of populations.

The objective of the present study was to investigate the impact of climatic variability and warming trend on all of the flatfish populations in the Bay of Biscay. The aim was here to complete the previous approaches by a global study on the entire flatfish community, linked to analyses on the process involved in the observed changes. Groundfish surveys provided data for twenty flatfish species caught in this area over the two last decades. Here we addressed the following questions: Do flatfish populations show long-term trends in abundance and occurrence? Is the interannual variability of abundance related to seawater temperature? What are the involved processes? We finally discussed the relative roles of climate warming and fishing pressure on flatfish populations.

A.III. Materials & Methods

A.III.1. Sea surface temperature (SST) in the Bay of Biscay for the two last decades

Sea surface temperatures were extracted from a database provided by the Hadley centre, Met Office (http://badc.nerc.ac.uk). These data were measured in situ from 1870 to present, each month, and satellite observations were included in the modern period. The data were interpolated on a 1° latitude–longitude spatial grid (Rayner et al. 2003). SST values were

extracted from this database from 1960 to 2006 from nodes of the grid located between 43.5°N and 47.5°N, and 1.5°W and 4.5°W (9 nodes located in the Bay of Biscay). Annual, summer (June–August) and winter (January–Mars) mean SST were calculated over this area.

Bottom temperature were not available on such a complete series but only on a restricted data set (Ifremer, unpub. data), consisting in summer mean temperatures (from June to August) at 100 m in depth in the Bay of Biscay from 1967 to 2002. A comparison between the common parts of the two data sets (mean temperatures from June to August between 1967 and 2002) was performed and a significant correlation was found (Pearson correlation coefficient r=0.68; n=36; P=10−5). This relation was obtained on summer data, when the maximum stratification of the water column occurs. The SST was thus assumed to represent interannual variations of temperatures in the water column on the continental shelf. We used the exhaustive SST time series to study trends inwater temperature in the Bay of Biscay and relations with flatfish densities.

A.III.2. Data from groundfish surveys over the Bay of Biscay shelf

17 groundfish surveys have been carried out annually since 1987 by Ifremer in the Bay of Biscay (Fig. A.1) from September to December (Souissi et al., 2001; Poulard and Trenkel, 2007). The survey area was located between 48°30′ N in the North and 43°15′ N in the South. The sampling scheme was stratified according to latitude and depth (Fig. A.1). A 36/47 otter trawl with a 20mmmesh codend linerwas used. Haulswere run for 30 min, with a towing speed of 4 knots. Fishingwas mainly limited to daylight hours. Catch numbers were recorded for all species, all finfish were measured. From 56 to 113 hauls were carried out per year (Fig. A.1) and provided data on the occurrence and abundance of twenty flatfish species.

Abundances (number of individuals per trawled surface, in hectare, for each species) were estimated on the stratified sampling scheme, with relation to mean density in each

depth×latitude area and to the surface of these areas, as described in Pennington & Grosslein (1977). As age compositionwas not available for the studied species from these surveys, all year classes were pooled to estimate abundance. The occurrence of each species was expressed as the relative number (in %) of positive hauls in a survey.

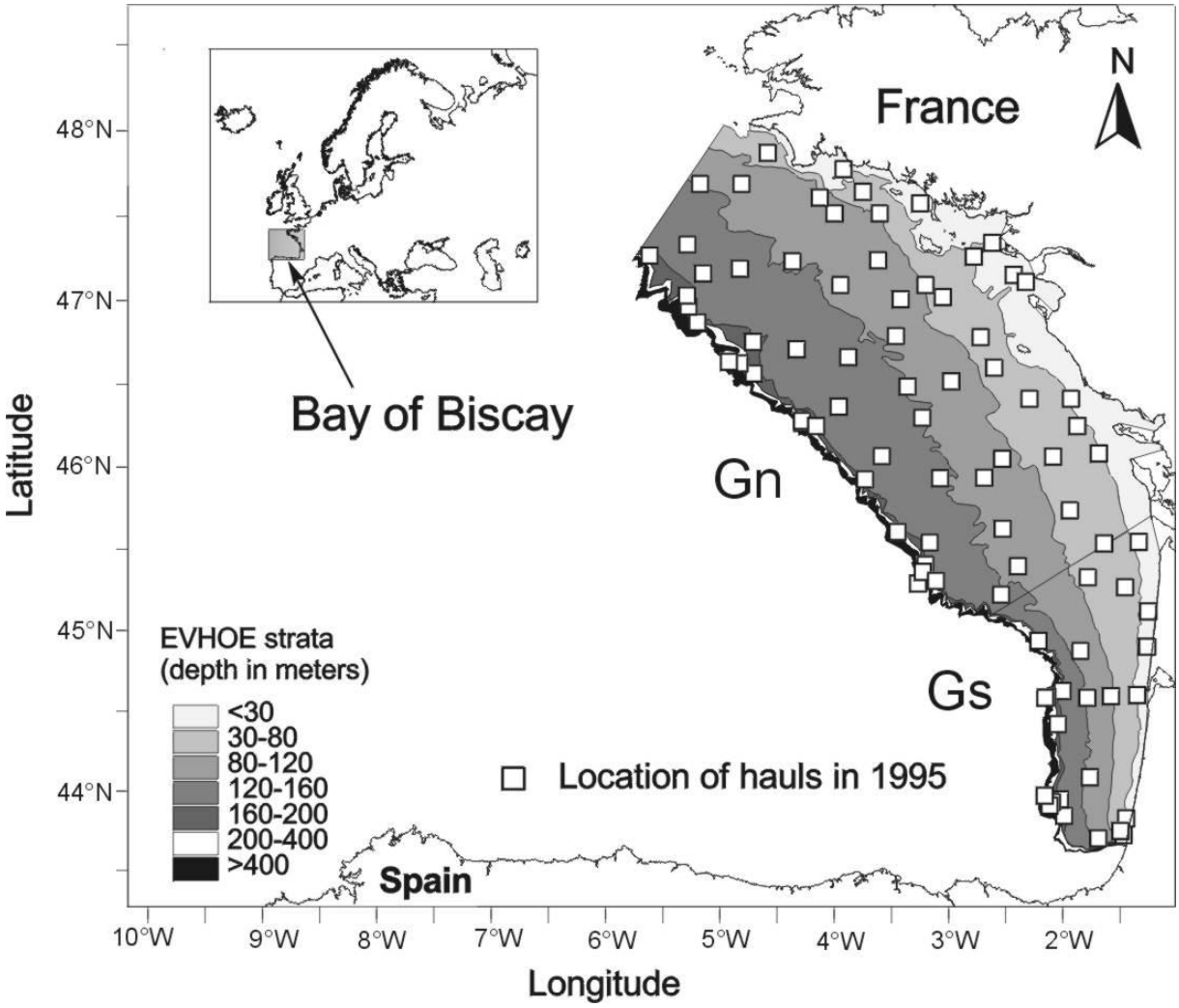

Figure A.1 Map of the Bay of Biscay, with its location in Europe in the upper left corner, showing the area sampled during the 17 groundfish surveys carried out by Ifremer from September to December since 1987, with the sampling design of 1995, given as example. The sampling schemewas stratified according to latitude (Gn, forNorth, and Gs, for South) and depth.

A.III.3. Flatfish species in the Bay of Biscay

Data were collected for the 20 flatfish species caught in the Bay of Biscay during this series of annual surveys (Table A.1). Mean latitudinal range of each species was estimated from the northern and southern limits of their geographic distribution according to the general description by Wheeler (1978), who provided a reference previous to the beginning of our time series, where geographic range were estimated at the same time for all the studied species. Moreover, thank to this mean latitudinal range, the 20 species were classed in three class of biogeography related to their mean latitudinal range (Table A.1) and to the location of the study site (Fig. A.1): southern species (b43.5°N), species centered in the Bay of Biscay (midrange species, [43.5–48°N]), northern species (N48°N).

Fishing effort was less known for most of the species in the Bay of Biscay. Exploitation level was described according to expert knowledge as a qualitative variable classified in 3 categories: (i) Commercial targeted species; (ii) Occasional commercial species, involuntarily caught in limited number with target species; (iii) Non-commercial species, rarely captured because they live in inaccessible environments for fishing gears and/or their size makes them unfit for commercialization.

Table A.1 Northern and southern limits of geographic distribution, mean latitude, latitudinal position with regard to the Bay of Biscay and exploitation level of the 20 caught flatfish species.

Species	Common name	Limits of distribution	Mean latitudinal range	Range classification for the Bay of Biscay	Exploitation level
Arnoglossus imperialis (Rafinesque, 1810)	Imperial scaldfish	58°N – 12°S	23°N	Southern species	Not commercial
Arnoglossus laterna (Walbaum, 1792)	Scaldfish	62°N – 30°N	46°N	Midrange species	Not commercial
Arnoglossus thori Kyle, 1913	Thor's scaldfish	54°N – 42°N	48°N	Midrange species	Not commercial
Bathysolea profundicola (Vaillant, 1888)	Deepwater sole	55°N – 17°S	19°N	Southern species	Not commercial
Buglossidium luteum (Risso, 1810)	Solenette	59°N – 17°S	21°N	Southern species	Not commercial
Dicologlossa cuneata (Moreau, 1881)	Wedge sole	47°N – 32°S	7.5°N	Southern species	Targeted
Lepidorhombus boscii (Risso, 1810)	Fourspot megrim	62°N – 31°N	46.5°N	Midrange species	Targeted
Lepidorhombus whiffiagonis (Walbaum, 1792)	Megrim	66°N – 34°N	50°N	Northern species	Targeted
Limanda limanda (Linnaeus, 1758)	Dab	71°N – 42°N	56.5°N	Northern species	Targeted
Microchirus variegatus (Donovan, 1808)	Thickback sole	58°N – 2°N	30°N	Southern species	Occasional
Microstomus kitt (Walbaum, 1792)	Lemon sole	70°N – 42°N	56°N	Northern species	Targeted
Phrynorhombus norvegicus (Günther, 1862)	Norwegian topknot	70°N – 47°N	58.5°N	Northern species	Not commercial
Platichthys flesus (Linnaeus, 1758)	Flounder	70°N – 30°N	50°N	Northern species	Not commercial
Pleuronectes platessa Linnaeus, 1758	Plaice	70°N – 30°N	50°N	Northern species	Targeted
Scophthalmus maximus (Linnaeus, 1758)	Turbot	65°N – 30°N	47.5°N	Midrange species	Targeted
Scophthalmus rhombus (Linnaeus, 1758)	Brill	62°N – 30°N	46°N	Midrange species	Targeted
Solea lascaris (Risso, 1810)	Sand sole	58°N – 33°S	12.5°N	Southern species	Occasional
Solea senegalensis Kaup, 1858	Senegalese sole	47°N – 14°N	30.5°N	Southern species	Occasional
Solea solea (Linnaeus, 1758)	Common sole	62°N – 27°N	44.5°N	Midrange species	Targeted
Zeugopterus punctatus (Bloch, 1787)	Topknot	64°N – 43°N	53.5°N	Northern species	Not commercial

A.III.4. Mean age of the catches by flatfish species

Mean age of the catches by flatfish species was determined according to the Von Bertalanffy growth equation:

$$\bar{t} = t0 - \frac{1}{K} \times \ln\left(\frac{L_\infty - \overline{L_t}}{L_\infty}\right) \quad (1)$$

where K is the growth rate (year^{-1}), L_∞ is the ultimate length of the catches (cm), L_t is the mean length of the catches for the considered species over all the years of the study (cm) and t_0 is the theoretical age for a length of 0 cm (years). K, L_∞ and t_0 were obtained from Fishbase database (www.fishbase.org).

A.III.5. Statistical analysis

A.III.5.1. Temporal trends in biological and environmental time series

We first analyzed the temporal trends in seawater temperature and in flatfish abundances and occurrences. A Kendall correlation test was used to check for correlation between the year and 3 SST indices (annual, summer and winter temperatures) and for correlation between the year and the annual abundances of each species. This non-parametric method was chosen because of the non-linear trends between the year and the studied responses variables (Fischer 2003). Temporal trends in SST were analysed over the whole time series (1960–2006) and over the period covering the study (1987–2006).

Some species were caught in low numbers (<10 ind. ha^{-1} year^{-1}) that may break up the trends in abundances. To complete the results on the abundances, we also checked the trends in occurrences. We used a logistic model to test correlation between the year and the annual occurrences of each species, given the binary nature of this variable (probability of presence).

A.III.5.2. Meta-analysis of these population trends

To synthesize the results, we realized a global analysis by pooling all the population trends in the same analysis (Planque & Fredou 1999). In that aim, we plotted the temporal slope obtained from the Kendall correlation test for each of the 20 species on their mean latitude. In such a metaanalysis, significant and unsignificant slope obtained for each population were compiled (Richardson & Schoeman 2004) to analyse the global response of flatfish populations with relation to their biogeographic distribution. Furthermore, we grouped populations with regards to their mean latitudinal range (Southern Biscay, Bay of Biscay, Northern Biscay, Table A.1) and we tested with an analysis of variance (AOV) if temporal trends differ among these categories. For each of these groups, we also tested with a student t-test, if the distribution of the temporal slopes differed from 0.

A.III.5.3. Correlations between SST and abundances time series

Interannual variability in the abundances of each species was related to annual mean SST. This comparison was performed with a time lag from 0 to 6 years between the two time series. Abundance of a given year was related to SST of the same year and to those of the 6 previous years.

Time series of annual mean SST and abundances were first compared using raw data. The correlations were then checked after removing trends and autocorrelation from the time series. Indeed, procedures for statistical testing of the correlation between the abundances and SST series must account for the autocorrelation (lowfrequency variability) and trends in the time series because they may result in an artificial increase in the statistical significance of the correlation test (Pyper & Peterman 1998). The aimwas to transform the original data to eliminate statistically significant trends and to account for autocorrelation whilst retaining the high-frequency signal (Fox et al. 2000). To assess correlations between SST and interannual

variations in abundances time series, we first removed the trends by prewhitening the data series prior to statistical testing. Prewhitening of the abundances and SST time series was performed by applying a linear model to times series and using residuals (calculated by the least squares method) in the correlations.We then adjusted the d.f. in the statistical tests to compensate for autocorrelation (Pyper & Peterman 1998). To adjust d.f., we applied the equation proposed by Chelton (1984) and modified by Pyper é Peterman (1998):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_j r_{xx}(j) r_{yy}(j) \tag{2}$$

where N* is the corrected sample size, considered as the number of independent joint observations on the two time series, X (abundance data) and Y (SST data), N is the length of the initial time series and r_{xx} (j), and r_{yy}(j) are the autocorrelation of X and Y at lag j. Estimators of autocorrelation r are obtained using the Box–Jenkins' equation (Box & Jenkins 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j} \times \frac{\sum_{t=1}^{N-j}(X_t - \overline{X})(X_{t+j} - \overline{X})}{\sum_{t=1}^{N}(X_t - \overline{X})^2} \tag{3}$$

where X is the overall mean.

Pyper & Peterman (1998) tested a variety of d.f. adjustment methods and found Eq. (2) to be robust and unbiased compared with other methods. This method is also robust to the number of lags applied in the d.f.-reduction (Eq. (2)). In the present analysis, we calculated autocorrelations until the fourth lag approximately equal to N/5, following Pyper & Peterman (1998). The correlation was then assessed using Pearson coefficients with d.f. correction for autocorrelation as described above (Eq. (2)). The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with N*−2d.f.

A.IV. Results

A.IV.1. SST increase in the Bay of Biscay

Kendall correlation tests showed an increase in annual, winter and summer mean SST over the period 1960–2006 (Table A.2). Similar trends were found for annual and summer mean SST in the recent period when fish data are available, between 1987 and 2006 (Fig. A.2; Table A.2).

Table 2 Coefficient and significance (ns: non significant; P > 5%) of the Kendall correlation between the year and the annual, winter and summer mean SST in the Bay of Biscay over the whole time series (1960-2006) and over the period covering the study (1987-2006).

	r	**P (in %)**
1960-2006		
Annual SST	0.38	< 0.1
Winter SST	0.22	2
Summer SST	0.42	< 0.1
1987-2006		
Annual SST	0.44	< 1
Winter SST	0.03	ns
Summer SST	0.51	2

A.IV.2. Changes in abundance/occurrence of flatfish populations with respect to latitudinal distribution

Over the 20 flatfish species caught during the study, 8 (40%) showed a significant change in their abundances and 9 (45%) in their occurrences (Table A.3). These two variables increased for the imperial scaldfish, the wedge sole and the thickback sole, whereas they decreased for the dab, the flounder and the plaice. The number of catches has dropped dramatically for the last 3 species since 1995 (1 dab, no flounder and 3 plaices).While the Norwegian topknot and the turbot showed a decrease only in their abundances, a clear increase in occurrence was

found for the scaldfish, the deepwater sole and the solenette. On the whole, among the 20 flatfish species studied in the Bay of Biscay, 5 species were in decline (in abundance and/or occurrence) and 6 in expansion.

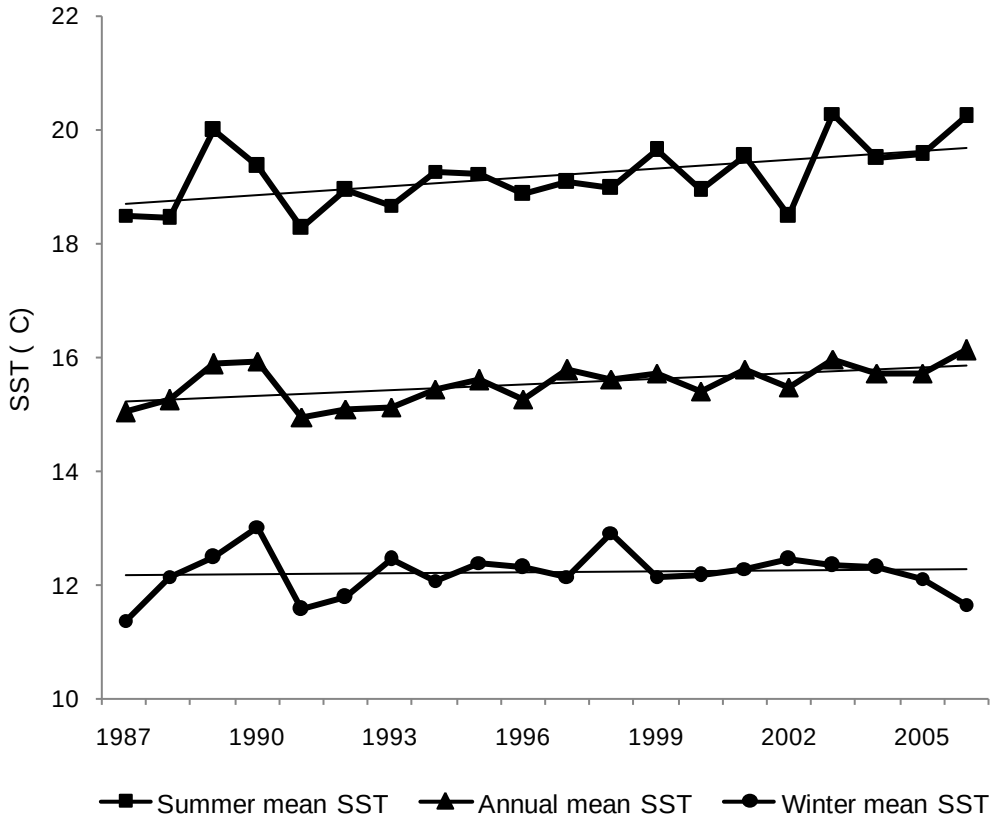

Figure A.2 Time series of the see surface temperature in the Bay of Biscay for four flatfish species in the Bay of Biscay since 1987.

When these results were considered with regards to species latitudinal range, they provided a general signal (Table A.3): the mean latitudinal ranges of 5 of the 6 increasing species were southern from the Bay of Biscay, the last one being centred in this Bay, while the mean distributions of the 5 declining species were located at higher latitude (Table A.1). The meta-analysis on the 20 species reinforced this general pattern (Fig. A.3): the slope of the temporal trend declined with increasing mean latitudinal range. If this linear relation between mean latitude and temporal slope was not significant, slope were different (AOV, Pb1%)

between southern, midrange and Northern species (Fig. A.4). Moreover t-test demonstrated that slopes were positive (Pb1%) for southern species, not significantly different from 0 for species centred in the Bay of Biscay and negative for northern species (Pb1%). These patterns were confirmed from species occurrence; even if levels of significance were different, both probability of catch and densities provided comparable results and the sign of the slope of the time trends was similar for the 20 species (Table A.3).

Table A.3 Trends in abundance and occurrence for the twenty flatfish species sampled over the continental shelf of the Bay of Biscay during the seventeen surveys conducted from 1987 to 2006. r: coefficient of the Kendall correlation between the year and the abundance, a: coefficient of the logistic regression between the year and the occurrence. P: significance in % (ns: unsignificant; P > 5%). Species are classified as northern, southern or midrange species for the Bay of Biscay according to their mean latitudinal range.

Species	**Abundance**		**Occurrence**	
	r	**P (in %)**	**a**	**P (in %)**
Northern species				
Phrynorhombus norvegicus	-0.40	3	-0.05	ns
Limanda limanda	-0.67	< 0.1	-0.25	< 0.1
Microstomus kitt	-0.29	ns	-0.01	ns
Zeugopterus punctatus	0.01	ns	0.03	ns
Lepidorhombus whiffiagonis	0.00	ns	-0.01	ns
Platichthys flesus	-0.57	< 1	-0.23	< 0.1
Pleuronectes platessa	-0.66	< 0.1	-0.17	< 0.1
Midrange species				
Arnoglossus thori	0.26	ns	0.11	ns
Scophthalmus maximus	-0.52	< 1	-0.06	ns
Lepidorhombus boscii	0.34	ns	0.02	ns
Arnoglossus laterna	0.29	ns	0.06	< 0.1
Scophthalmus rhombus	-0.09	ns	-0.07	ns
Solea solea	0.10	ns	0.01	ns
Southern species				
Solea senegalensis	0.20	ns	0.20	ns
Microchirus variegatus	0.43	2	0.09	< 0.1
Arnoglossus imperialis	0.49	< 1	0.08	< 0.1
Bathysolea profundicola	0.12	ns	0.09	< 1
Buglossidium luteum	0.08	ns	0.04	1
Solea lascaris	-0.02	ns	0.03	ns
Dicologlossa cuneata	0.37	4	0.04	< 1

r: coefficient of the Kendall correlation between the year and the abundance, a: coefficient of the logistic regression between the year and the occurrence. P: significance in % (ns: unsignificant; PN5%). Species are classified as northern, southern or midrange species for the Bay of Biscay according to their mean latitudinal range.

Regarding the level of exploitation of these species, non-commercial, occasional and target species were all distributed on the whole latitudinal range but the proportion of targeted species increased with latitude (Fig. A.3). 3 of the 5 northern significantly declining species appeared to be targeted but 4 of the 6 southern species in expansion were non-commercial species (Table A.1). When all the species were taken into account (Fig. A.3), there were no discrepancies in the relation between latitudinal range and temporal trends with regards to the level of exploitation.

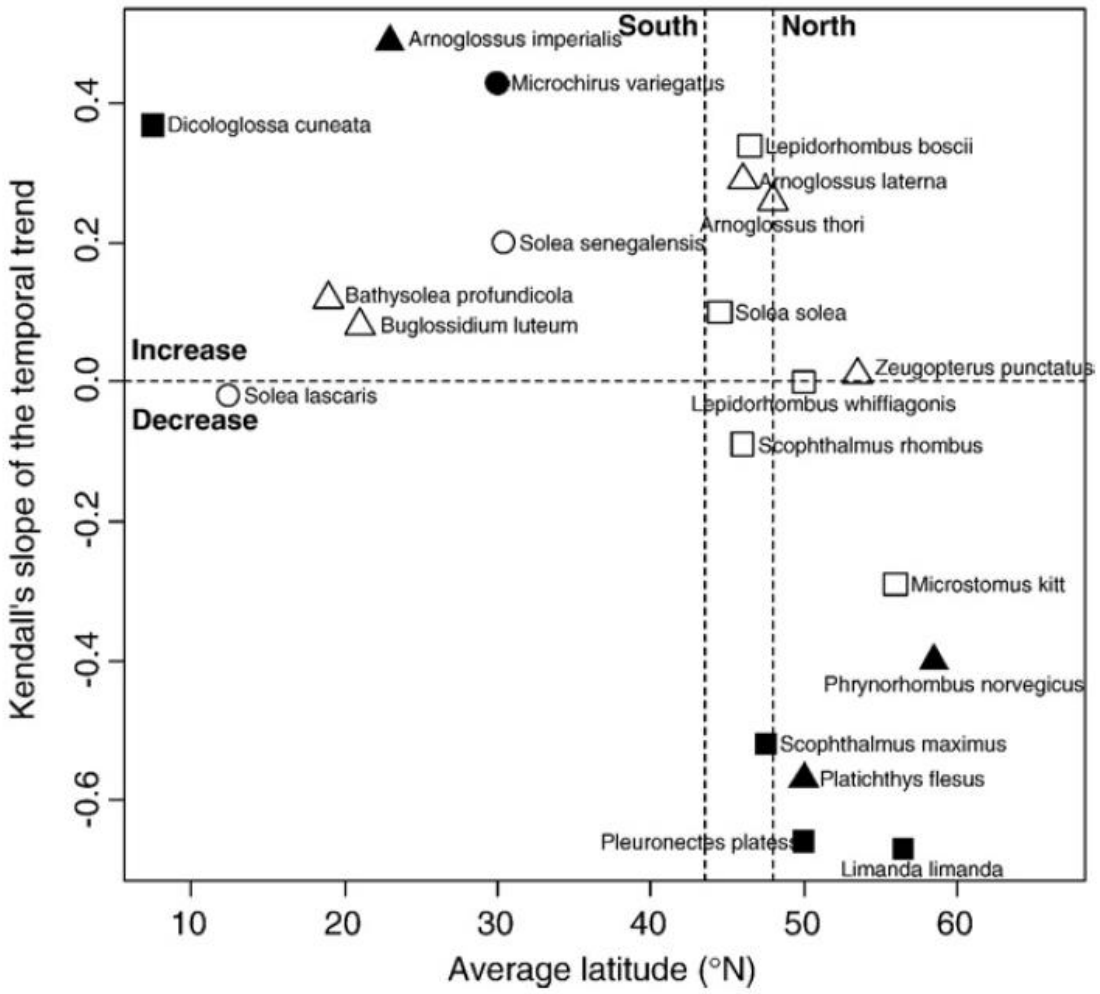

Figure A.3 Relation between the Kendall's slope of the temporal trend in fish densities since 1987 and the mean latitudinal range for the 20 flatfish species caught in the Bay of Biscay. Horizontal dotted line: limit between negative and positive temporal trend; vertical lines: southern and northern limits of the Bay of Biscay. Species are identified with symbols related to their level of exploitation: triangle: not commercial, circle: occasional, square: targeted. Filled symbol corresponds to significant slopes.

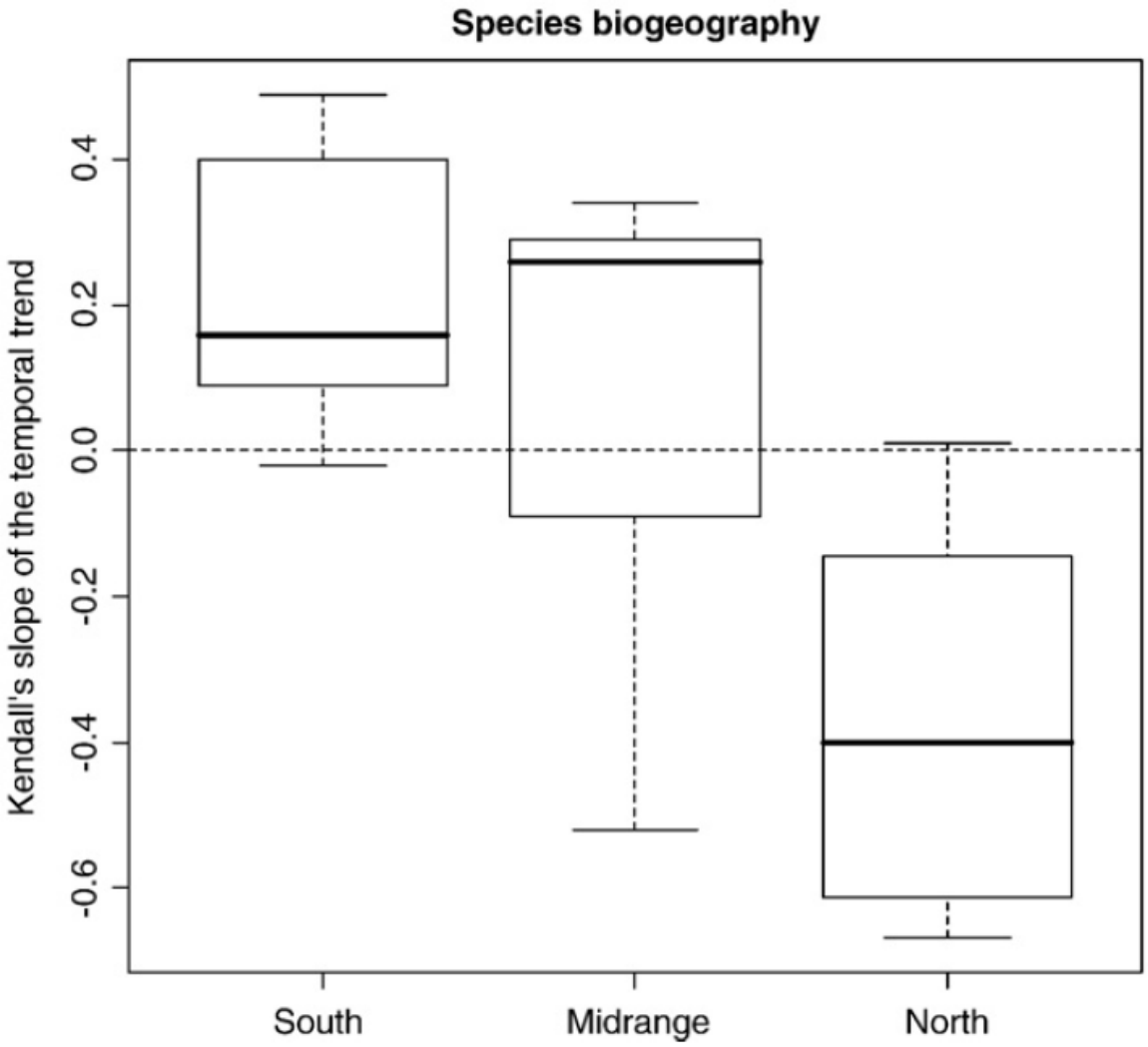

Figure A.4 Boxplots of the distribution of the Kendall's slopes of the temporal trend in fish densities since 1987 for the three groups of flatfish species (southern, centred in the Bay of Biscay, northern).

A.IV.3. Influence of annual mean SST on abundance of flatfish species

Relation between time series of annual mean SST and abundances were first analysed without removing trends and significant relations were obtained for 5 species (Fig. A.5a). For 4 species, the highest correlation between annual mean SST and abundanceswas found for a lag equal to the mean age of the population, as calculated with the mean size of the catches and the von Bertalanffy growth equation (Fig. A.5a). A different pattern was found for the plaice. This population with ameanage of 3 years showed amaximumcorrelation coefficient for a lag

of one year (r=−0.76), but correlation coefficients for lags of 2 and 3 years remain close to the maximum value (r=−0.71 and r=−0.75 respectively).

The correlations were then checked after removing trends and autocorrelation in the timeseries (Fig. A.5b). Correlations between annual mean SSTand abundanceswere significant for the imperial scaldfish and the turbot for a lag equal to the mean age of the populations.

Systematically, correlations between temperatures and abundances were negative for the declining species distributed in the north of the Bay of Biscay and positive for the expanding species distributed in the south of the bay (Fig. A.5).

A.V. Discussion

A.V.1. Seawater warming in the Bay of Biscay

The present study indicated a significant increase in annual, summer and winter SST over the whole continental shelf of the Bay of Biscay since 1960. These results were consistent with those obtained at a global scale on the consequences of warming in the coastal zone (Sundermann et al. 2001) and with the previous studies which described a seawaterwarming in the southern part of the Bay of Biscay since the 70s (Koutsikopoulos et al. 1998; Planque et al. 2003), then in the northern part since the 80s (Désaunay et al. 2006). In a study outside the continental shelf of the Bay of Biscay, Blanchard & Vandermeirsch (2005) specified that warming affects the entirewater column, with an increase in sea temperature of 0.8 °C between 50 and 200 m over the period 1970–2000. The preliminary analysis realized here on available bottom temperature on the continental shelf also demonstrated that variations in surface temperature also affect the bottom layer. Therefore, this warming impacts the habitat of flatfishes which live in the bottom waters of the continental shelf.

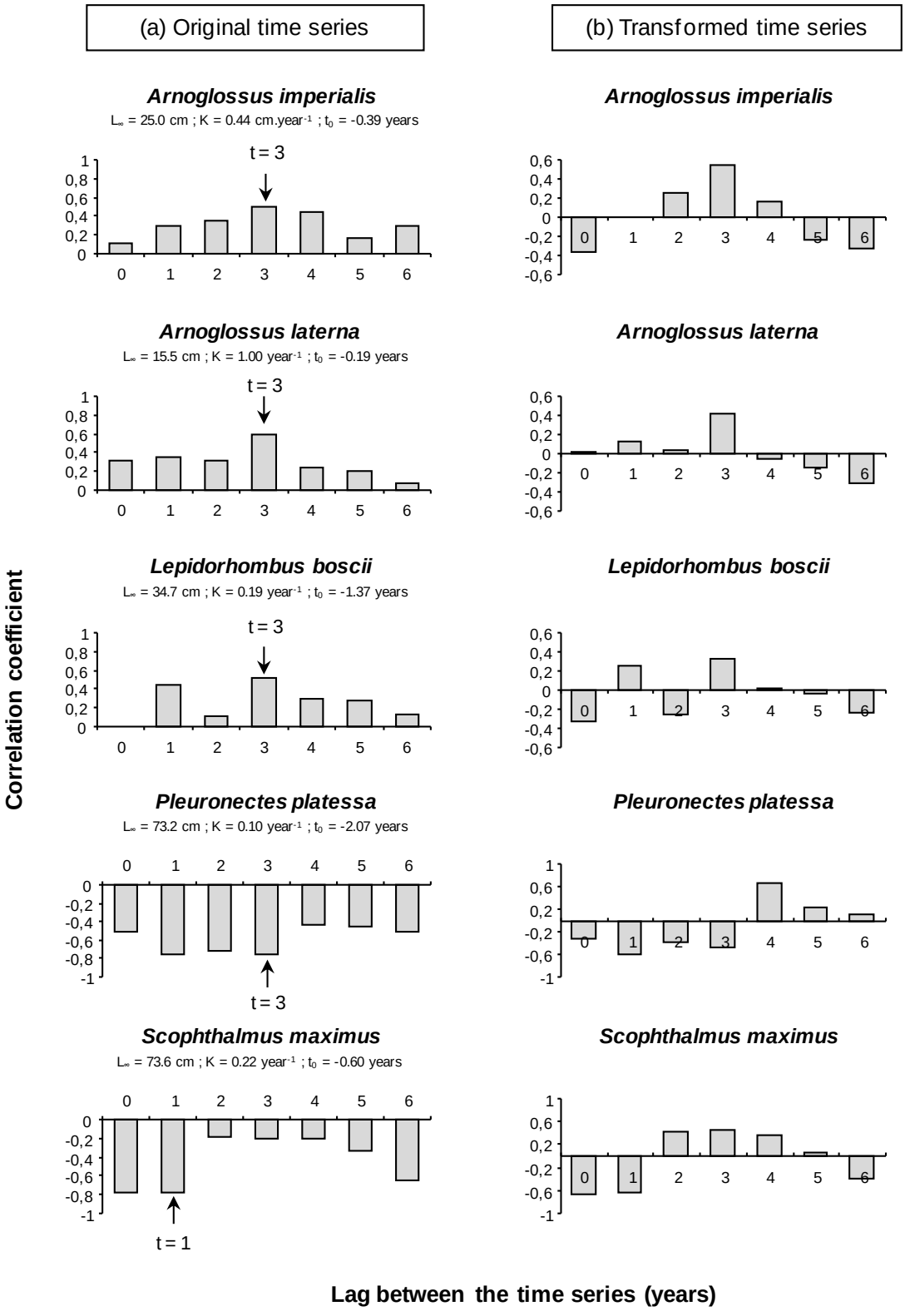

Figure A.5 Coefficients of the linear correlation between mean annual SST and flatfish abundances with a lag from 0 to 6 years between the two time series, using (a) original data and (b) transformed data (after removing trends and autocorrelation). t is the mean age of the populations (expressed in years). Parameters of the Von Bertalanffy growth equation used to calculate this mean age are indicated for each species on part (a).

A.5.2. Impact of warming on flatfish populations

A.5.2.1. Trends in abundance and occurrence with regards to geographical distribution

The impact of warming on flatfish populations in the Bay of Biscay was demonstrated through the latitudinal distribution of the affected species. It is important to notice that the approximates of the latitudinal range taken from Wheeler (1978) could be cautious for some species. Nevertheless, these data were used to estimate a mean latitudinal range for a metaanalysis and they provided imprecise but standardized and simultaneous approximates. The mean latitudinal ranges of the 5 declining species were between 47.5°N and 58.5°N, those of the 6 expanding species between 7.5°N and 46°N. This clearly indicated a rarefaction of the northern species and an expansion of the southern ones with a limit in the Bay of Biscay (43.5–48°N). More precisely, the mean latitudinal range of 4 over the 5 declining species was northern than the Bay of Biscay. For the last one, it was located at the North of this Bay. These northern species have a preference for cold waters. For instance, the plaice favours temperatures between 2 and 15 °C (Fox et al. 2000). By contrast, among the 6 expanding species, the mean latitudinal distribution of the scaldfish was located in the Bay of Biscay but, for the 5 other species, it was largely more southern. Some of them, such as the imperial scaldfish and the wedge sole, could be described as sub-tropical species, as their distribution extends until southern hemisphere. Southern species are thus adapted to cope with higher temperatures. Moreover, this conclusion appeared consistent when all the species were taken into account; the trends demonstrated on species for which significant results were obtained were reinforced by metaanalysis. The pattern of increasing southern species and decreasing northern species appeared general with this method previously validated to analyse trends in primary production with regards to climate change worldwide (Richardson & Schoeman 2004).

While the northern temperate species distribution retreated northwards to avoid the temperature increase, the southern temperate species took advantage of seawater warming to spread over the Bay of Biscay. These processes have already been highlighted in the North Atlantic. Quéro et al. (1998) have first noted an increase in abundance of tropical species in the south of the Bay of Biscay and a northward shift of these species from 16° to 30°N since 1965, some of them until the Irish Sea. Perry et al. (2005) showed a significant change in mean latitudes in relation to warming for 15 fish species in the North Sea. Their center of distribution moved from 48 to 403 km over the last 25 years and most of these shifts were northward. They notably indicated polar shifts for the scaldfish, the dab and the common sole. In the same way, several studies have reported successive northward and southwards migrations in cod (*Gadus morhua*) caused by alternating events of warming and cooling of North Atlantic seawater since the beginning of the 20th century (Drinkwater 2005). Thus, northward redistribution, or polar drift, appeared as a response to climate change of flatfish species according to their temperature requirements (Stebbing et al. 2002; Perry et al. 2005; Drinkwater 2005). Because most of fish species tend to prefer a specific range of temperature, changes of geographical distribution of species often match with long-term changes in temperature. In the northern hemisphere, seawater warming induced a northward shift of fish distributions (Rose 2005).

A.5.2.2. Relationships between temperature and abundance

To estimate the short-term impact of warming on flatfish populations in the Bay of Biscay, we performed comparisons between temperature and abundance time series. Then, we compared the time lags (in years) in correlation with the mean age in the population. Without age determinations from otoliths, this mean age was roughly estimated from growth parameters taken from fishbase and this method only provided an uncertain qualitative estimate. With

transformed data (removed trend and autocorrelation), few (2 species) significant correlations were obtained, as the short-term effect could be hidden by (i) the pool of several cohorts in abundance indices, and subsequent autocorrelation in abundance time series and (ii) variability unexplained by temperature and uncertainty in estimates related to surveys (Poulard & Trenkel 2007). Moreover, variability in flatfish abundance is related to the long-term changes in temperature and a comparison between abundance and SST time series by smoothing the data would be appropriate to observe lowfrequency variability (Fox et al. 2000). However, such methodwas not appropriate here because of the shortness of the series. The solution was hence to compare the series while trends were preserved. Using this approach, correlation coefficients result from the combination of both long-term changes (low-frequency variability and, easily viewable here, trend) and short-term changes (high-frequency variability). Even if these correlations could not be used to test the relation between temperature and abundance, because their significance was over-estimated by temporal autocorrelation, they provided an indication of the covariations.When trends were preserved, species showed the highest correlation for a time lag close or equal to the estimated mean age of the population. The same pattern was obtained with the transformed series for 2 of these 5 species, also with significant correlations for a lag equal to the mean age of the population. Furthermore, with regards to warming, these correlations were consistent to the results on temporal trends in abundance and occurrence: they were negative for the northern temperate species and positive for the southern ones. These results suggested that flatfish abundance is related to temperature in their year of birth.

A.5.2.3. Response of flatfish population to temperature increase: a consequence of changes in recruitment

The northward redistribution of flatfish species in the Bay of Biscay could be explained by two processes. First, the individuals could migrate to follow their temperature range. However, such migrations are unlikely for flatfishes as they are quite sedentary, their movements being reduced and essentially seasonal. Adults migrate to deeper waters in winter to reproduce and come back inshore in summer to feed (Deniel 1981; Quéro & Vayne 1997). Secondly, the response of species to climate change could depend on the success of the different phases of their life cycle (Rose 2005; Wood et al. 2002). The recruitment is one of the key stages which could be affected by temperature (Henderson1998; Philippart et al.1998; Fox et al. 2000) and its variability strongly influences the population structure (Levin & Stunz 2005). For a large proportion of flatfish species, the recruitment and the growth of juveniles occur in coastal nurseries (Gibson 1994). A disturbance in recruitment impacts the adult abundance at the end of the time needed for the juveniles to join adult population over the continental shelf, i.e. several years after. In the present study, for 40% of species which densities have changed, noticeable correlation was found between abundances and temperatures and the highest correlations were obtained for a time lag equal to the mean age of the population. Moreover, these correlations were positive for southern species and negative for northern ones. It indicated that abundances of adult flatfishes depend on temperatures in their year of birth and emphasized the impact of warming on recruitment.

This hypothesis of the effects of warming on the recruitment could also be highlighted for species of which abundance sharply decreased and quite disappeared from the catches before the end of the time series (plaice and dab). Désaunay et al. (2006) estimated the abundance of flatfish juveniles in the Bay of Vilaine nursery ground over the period 1981–2001. They indicated a drop in juvenile captures for the plaice and the dab since 1990 and 1993

respectively. As observed in the present study, adult abundance of both species decreased in the Bay of Biscay from 1995. This abundance drop could not arise from a northward migration of individuals, because the disappearance of juveniles and adults was not synchronous. For these 2 northern temperate species, the strong reduction of the adult abundance in the Bay of Biscay seems rather to be the consequence, with a time lag of several years, of a disruption of recruitment related to temperature rising. Brunel & Boucher (2007) led to the same conclusion about the major effect of warming on exploited fish population recruitment in the North Atlantic.

Therefore, in response to seawater warming, delayed trends in abundance time series between juvenile nursery grounds and adults on the continental shelf, and correlations between abundances and temperature in the year of birth, indicated a northward redistribution of flatfishes in the Bay of Biscay induced by changes that subsequently affect the recruitment success.

A.5.2.4. Ecological explanations of the effect of warming on flatfish recruitment

Seawater temperature affects metabolic and physiological rates, behaviour and hence population dynamics of fish (Brander et al. 2003). Fish recruitment is especially affected by seawater warming (Philippart et al. 1998; Fox et al. 2000; Clark & Hare 2002). Recruitment may be affected by sea temperature through (i) metabolic costs of spawners (Fischer 2003; Gibson 2005), (ii) eggs development (Van der Land 1991; Dethlefsen et al. 1996), (iii) activity of predators that feed on fish eggs and larvae (Wood et al. 2002), (iv) natural mortality of eggs and larvae (Van der Veer et al. 2000), (v) food availability (Cushing 1990; Miller et al. 1991; Houde 1997; Mountain, 2002; Clark & Hare 2002) and, thus, growth (Fonds 1979) and survival (Suthers 1998) of larvae but also (vi) growth (Fonds 1975; Yamashita et al. 2001; Lekve et al. 2002; Le Pape et al. 2003; Tresher et al. 2007; Teal et al.

2008) and mortality of juveniles (Miller et al. 1988; Suthers 1998). Thus, many behavioral and physiological processes during spawning and larval phase may be affected by seawater warming.

Thus, the early life history stages of flatfish species are sensitive to seawater temperature (Fonds 1979). The list of temperature dependent factors influencing recruitment is extensive (see overview in Cushing 1995) and it is difficult to analyze the process involved in the consequences of sea warming. The relative importance of regulating factors on recruitment success differs according to species and region (see overview in Van der Veer et al. 2000), as fish populations respond to different predominant mechanisms (Nash and Geffen 2000; Désaunay et al. 2006). In the Bay of Biscay, as in other temperate areas, the influence of warming on recruitment success probably differs for sub-tropical and cold-temperate species (Wood et al. 2002). One relevant hypothesis to explain patterns of changes in the Bay of Biscay refers to the differences in life cycle of flatfish with regard to their latitudinal range. While cold northern flatfishes spawn during the winter–spring season, warm southern species spawn during spring–summer. These features were verified for the flatfishes that exhibit significant trends in the Bay of Biscay; except for the deep water sole (spawning season unknown), all the southern species spawn in spring–summer and the northern species in winter–spring (Wheeler1969; Legett & Frank, 1997; Désaunay et al. 2006). During winter, as metabolic costs of spawners are generally optimized for a temperature lower than the thermal optimum for the growth of young stages (Fischer 2003; Munday et al. 2008), sea warming negatively influences the recruitment of winter–spring spawning northern species. Especially, Van der Veer (1986) and Fox et al. (2000) showed a negative relationship between winter sea temperature at the time of spawning and the year-class strength of the plaice around the British Isles and in the North Sea. A similar relationship has been demonstrated for the dab in the Bristol Channel by Henderson (1998). On the contrary, winter growth of benthic juveniles

of southern spring– summer spawners could have been enhanced by winter warming and this faster growth would have increased their survival (Suthers1998). The pelagic larval phase of spring–summer spawning southern species was however not modified, because summer warming is below their (warm) maximal spawning thermal range. In the same time, increase in the summer growth of northern winter–spring spawning juveniles (Le Pape et al., 2003) seemed not to compensate more consequent losses (Van der Veer et al. 2000; Levin & Stunz 2005) related to the previous phase of the life cycle (winter–spring spawning, hatching and pelagic larvae). Hence, a shift could have occurred between increase of southern warm species and decline of northern cold ones with relation to their different life cycle.

A.5.3. Impact of fishing on flatfish populations

The study of changes in abundance and occurrence of flatfish populations in the Bay of Biscay cannot ignore the effect of fishing. Quéro & Cendrero (1996) have collected large amount of data about catches of fishes in the Arcachon basin (south of the Bay of Biscay). They indicated that the turbot, the brill, the plaice, the common sole and the wedge sole are targeted commercial species and they specified that the Senegalese sole, the sand sole and the thickback sole are often caught and confused with the common sole. These indications confirmed the categories of exploitation level that have been established in this study, according to specialists (Table A.1). This classification showed that among the 6 northern temperate species which have significantly dropped in abundance, 4 are target species for fishing and 2 are non-commercial. In contrast, among the 5 southern temperate species which have significantly increased, 3 are non-commercial and 2 undergo a targeted or occasional exploitation. The impact of fishing on flatfish populations tends therefore to combine with climate change (Gibson 2005), with a reduction of abundance for 45% of the large northern exploited species and an increase for 50% of the small southern non-commercial species.

However, as abundances decreased also for 25% of non-commercial species and increased for 11% of target species, a more general impact of warming could be pointed out; when all of the flatfish populations were considered in the metaanalysis, no difference in trends with regard to the level of exploitation appeared on the 20 species. Nonetheless, target species appeared in a larger proportion in Northern than in Southern species. This last result appeared related to previous conclusions of Pauly (1994) and Van der Veer et al. (2003): the replacement of sub-polar species by tropical ones will result in higher occurrences of small flatfish species of less commercial interest. Thus climate changes can explain different trends between target and commercial flatfish. Nevertheless, fishing pressure can increase this pattern threw overexploitation of commercial species and also threwreduction of higher levels of the foodwebs (Pauly et al. 1998) and lower predation on small southern species.

A.6. Conclusion

Trawl survey data collected in the Bay of Biscay during the two last decades enabled us to show a significant variation in abundance for 55% of the flatfish species. The impact of climate change was evident with regard to the latitudinal range of population because the species in decline have their center of distribution northernmost than species in expansion, with a limit in the Bay of Biscay. This was a generalization of the previous results on 4 commercial flatfish species (Désaunay et al. 2006); it confirmed changes in species composition of fish communities (Poulard and Blanchard 2005) and demonstrated a general pattern of increase of southern species and decrease of northern ones. The analysis of abundance time series suggested an effect of seawater warming on recruitment. Indeed, for northern temperate species, the recruitment reduction occurred several years before the adult abundance decrease. Moreover, the correlation between abundances of species and the temperature in their year of birth emphasized this assumption. Nevertheless, although the

impact of seawater warming on flatfish populations in the Bay of Biscay was established, processes remain uncertain and are probably different between southern and northern species.

The impact of climate change on flatfish populations seemed to be amplified by fishing (Brander 2005), with a stock reduction in exploited species and an expansion of non-commercial species.

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Résumé

La réponse des traits à l'environnement a été étudiée essentiellement à travers la moyenne des attributs de trait des espèces et des lignées et a récemment été étendue à la variabilité intraspécifique. Cependant, les traits peuvent également répondre aux contraintes de l'environnement par (i) une forte détermination mutuelle des traits au sein des individus ou des populations, i.e. une forte intégration phénotypique, et (ii) une faible variation des traits au sein de lignées phylogénétiques entières. Nous avons testé : (i) les effets de l'environnement abiotique et biotique sur l'intégration phénotypique chez des espèces végétales subantarctiques et les conséquences écologiques et biogéographiques d'une forte intégration phénotypique, et (ii) les effets de l'environnement abiotique et biotique sur la variabilité phénotypique réalisée au sein des genres d'Angiospermes de l'Europe Centrale. Pour le premier aspect, nous avons constaté que l'intégration phénotypique est plus forte en conditions abiotiques stressantes. Le renforcement de l'intégration phénotypique se produit sur de petites échelles spatiales et peut limiter la flexibilité à grande échelle des stratégies de croissance et de reproduction. Nous avons également montré que la forte intégration phénotypique et environnementale peut contribuer à l'endémisme de certaines espèces subantarctiques, probablement par une spécialisation sur le long terme de ces espèces à leur habitat. Pour le second aspect, nous avons observé que la variabilité phénotypique réalisée au sein des genres de l'Europe Centrale est plus élevée dans des conditions abiotiques intermédiaires, ce qui reflète une plus grande indépendance des traits vis-à-vis de l'environnement abiotique. Nous avons également montré que le nombre d'espèces en coexistence est très conservé au sein des genres. Un niveau intermédiaire de coexistence semble coïncider avec à la fois une position intermédiaire des genres le long de gradients abiotiques et une plus grande variabilité de certains traits. Ceci suggère un rôle des interactions biotiques nombreuses, mais toujours prévisibles, pour le maintien (ou l'évolution) de niveaux élevés de variabilité des traits au sein des clades. Finalement, l'ensemble de nos résultats suggèrent que la capacité des espèces à répondre aux variations de l'environnement pourrait être fortement limitée aussi bien au niveau des phénotypes individuels qu'à l'échelle des clades entiers, notamment dans des environnements abiotiques et biotiques extrêmes.

Mots Clés: traits d'histoire de vie, intégration phénotypique, variabilité phénotypique réalisée, endémisme, gradients abiotiques, coexistence et interaction des espèces, Angiospermes, clades, îles subantarctiques, Europe Centrale.

Abstract

The response of traits to the environment has been studied mainly at the level of trait means within and across species and lineages and has recently been extended to intraspecific trait variability. However, traits may respond to the constraints of a given environment also in terms of (i) increased mutual determination of traits within individuals and populations, i.e. increased phenotypic integration, and (ii) decreased variation of traits within entire phylogenetic lineages. Here we tested: (i) the effects of abiotic and biotic environments on phenotypic integration within sub-Antarctic plant species and the ecological and biogeographic consequences of a strong phenotypic integration, and (ii) the effects of abiotic and biotic environments on the phenotypic variability realized within Angiosperm genera of Central Europe. Regarding the first aspect, we found that phenotypic integration is higher under stressful abiotic conditions. The increase in phenotypic integration occurs at small spatial scales and may constrain the large scale flexibility of growth and reproductive strategies. We also found that strong phenotypic and environmental integration may contribute to endemism of some sub-Antarctic species, probably through a long-term specialization of these species to their habitat. Regarding the second aspect, we found that phenotypic variability realized within genera of Central Europe is higher under intermediate abiotic conditions, reflecting increased independence of traits from the abiotic environment. We also found that the number of coexisting species is highly conserved within genera. Intermediate levels of coexistence tend to correspond to both intermediate positions along abiotic gradients and to highest levels of variability of certain traits. This suggests a role of numerous but still predictable biotic interactions for the maintenance (or evolution) of high levels of trait variability within clades. Overall, the results of both aspects suggest the capacity of species to respond to environmental variations may be strongly constrained at the level of both individual phenotypes and entire clades, notably under abiotically but also biotically extreme environments.

Key-words: life-history traits, phenotypic integration, realized phenotypic variability, endemism, abiotic gradients, species coexistence and interaction, Angiosperms, clades, sub-Antarctic Islands, Central Europe.